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## Autosome

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## Synonyms

[Euchromosome](#); [Somatic chromosome](#)

## Definition

All chromosomes except the sex chromosomes are referred to as autosomes. They exist in pairs in the somatic cells whereas singly in the gametic cells.

## Introduction

Chromosomes can be categorized in two categories – autosomes and allosomes (sex chromosomes). All the chromosomes other than the sex chromosomes are autosomes. For example, in case of human diploid genome, 44 autosomes (22 pairs) are present along with 2 allosomes (a normal female will have a pair of X chromosome whereas a normal male will have a pair of X and Y chromosome). Autosomes have been numbered on the basis of their sizes from 1–22 in the human genome in contrast to the letters (X and Y) used

for the allosomes. Genes located on these autosomes affect males and females in the same way (Ohno 2013). Another striking property of autosomes is that they are homomorphic, i.e., the position of the centromere is identical unlike the case of the male sex chromosome which is heteromorphic (Fig. 1).

The evolutionary processes in case of autosomes are fueled by homologous recombination and mutation.

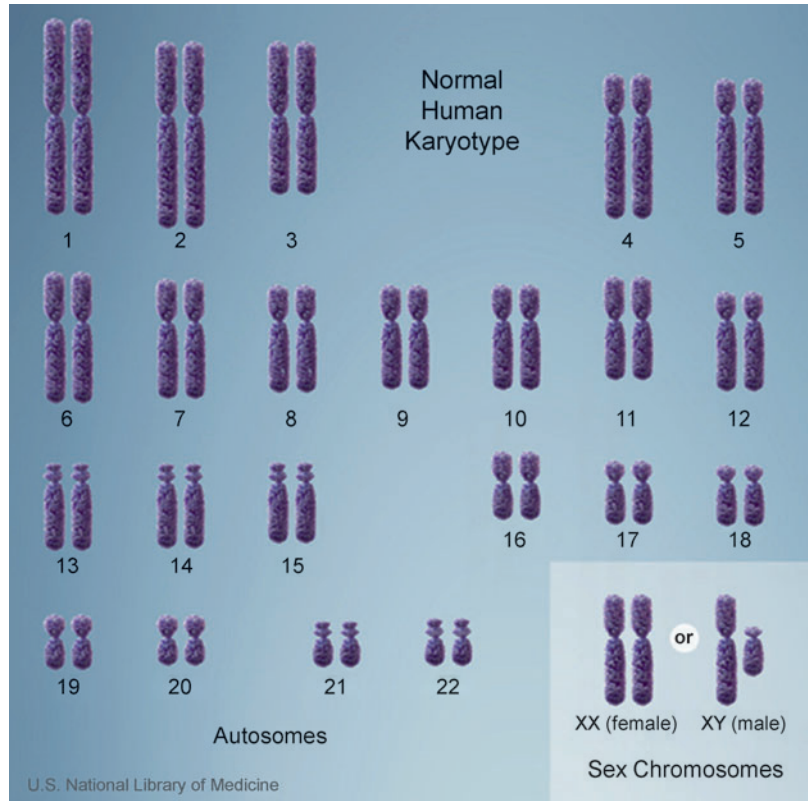
## Mapping of Autosomes

The mapping and identification of the human chromosomes is performed by extracting the chromosomes from a cell that has been arrested in the metaphase or prometaphase followed by their staining with the suitable dye (Alberts et al. 2002; Craig and Bickmore 1993). These stained chromosomes are further arranged in the standard format on the basis of their size and position of the centromere in chromosomes called as karyogram or ideogram.

The utility of this type of arrangement is that large-scale aberrations can be easily identified on comparison of the karyogram of a diseased person to that of a normal person (Therman and Susman 2012). Chromatic aberrations are the resultant of missing, extra, or irregular portion of the chromosomal DNA. Chromosomal aberration can occur in both autosomes and allosomes, but most abundantly they are found in autosomes in the form

### Autosome,

**Fig. 1** Figure depicting normal human karyotype. Homomorphic nature of the autosomes and heteromorphic nature of the male sex chromosome is clearly evident from this figure (Credit: U.S. National Library of Medicine (National Library of Medicine 2017))



of monosomies and trisomies ([http://anthro.palomar.edu/abnormal/abnormal\\_4.htm](http://anthro.palomar.edu/abnormal/abnormal_4.htm)).

### Monosomies

In case of a normal human being the total number of chromosomes should be 46 (44 + XY or 44 + XX). But a patient suffering from a monosomy of a particular autosome would have one copy less (43 + XY or 43 + XX) than the original chromosome number.

Cri du chat syndrome is an example of the monosomy in humans. It occurs due to the partial deletion of the end of the short p arm of chromosome number 5. The disease has been named as such because the person affected undergoes a malformed larynx which leads to distinctive cat-like voice (Niebuhr 1978).

### Trisomies

In trisomies of autosomes, one additional copy of an autosome is present (45 + XY or 45 + XX).

Down's syndrome is a very common autosomal trisomy disorder of chromosome number 21. The symptoms range from mild to moderate mental retardation along with some distinct physical traits (<https://www.cdc.gov/ncbddd/birthdefects/downsyndrome.html>). More examples are Edward's syndrome, which occurs due to the trisomy of chromosome number 18, and Patau syndrome, which occurs due to the trisomy of chromosome number 13. Apart from this, trisomy of chromosome numbers 9, 8, and 22 also occur.

### Autosomal Inheritance

The pattern of inheritance wherein transmission of alleles, present on autosomes, occurs is referred to as autosomal inheritance. This type of inheritance pattern is generally categorized into two types: autosomal dominant and autosomal recessive inheritance. In autosomal dominant disorders the mutated gene is dominant. In this condition only

one copy of the mutated gene is required to be affected by the disorder. Huntington disease and Marfan syndrome follow this inheritance pattern. In autosomal recessive condition, both copies of the gene are mutated. These disorders occur when both parents are carriers. Two carriers have a 25% chance of having an unaffected child who is also a carrier and a 25% chance of having an affected child with two recessive genes. Cystic fibrosis and Sickle cell disease follow this kind of inheritance pattern. (<https://ghr.nlm.nih.gov/primer/inheritance/inheritancepatterns>).

## Conclusion

Autosomes are the chromosomes having genes for anything that is not related with sex determination. They carry genes that control somatic traits and are different from the chromosomes governing the sex determination in a lot of aspects. Each pair of autosomes is identical genetically and morphologically. Humans have 22 pairs of autosomes which are numbered from 1 to 22 depending upon their size. Chromosome 1 has approximately 2800 genes while chromosome number 22 has around 750 genes. Mutations in the autosomal chromosomes lead to different kind aberrations like monosomies and trisomies of that particular chromosome. Furthermore, in case of mutations of the genes present on autosomes, the nature of the gene determines the pattern of inheritance that would be followed.

## Cross-References

- ▶ [Chromosome Mapping](#)
- ▶ [Human Diploid Genome](#)
- ▶ [Karyogram](#)

## References

- Alberts, B., Johnson, A., Lewis, J., Raff, M., Roberts, K., & Walter, P. (2002). *Molecular biology of the cell* (4th ed.). London: Garland Science, Taylor and Francis.
- Craig, J. M., & Bickmore, W. A. (1993). Genes and genomes: Chromosome bands—flavours to savour. *Bioessays*, *15*, 349–354.
- Niebuhr, E. (1978). The cri du chat syndrome. *Human Genetics*, *44*, 227–275.
- Ohno, S. (2013). *Sex chromosomes and sex-linked genes* (Vol. 1). Berlin: Springer Science & Business Media.
- Therman, E., & Susman, M. (2012). *Human chromosomes: Structure, behavior, and effects*. New York: Springer Science & Business Media.

## Web References

- [http://anthro.palomar.edu/abnormal/abnormal\\_4.htm](http://anthro.palomar.edu/abnormal/abnormal_4.htm)
- <https://ghr.nlm.nih.gov/primer/inheritance/inheritancepatterns>
- <https://www.cdc.gov/ncbddd/birthdefects/downsyndrome.html>
- Illustration: National Library of Medicine (US). (2017). *Genetics home reference*. Bethesda: The Library. Normal Human Karyotype; cited 2017 19 May. Available from: <https://ghr.nlm.nih.gov/handbook/illustrations/normalkaryotype.jpg>.

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## Promiscuity

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### Definition

Indiscriminate mating with multiple partners

### What Is Promiscuity?

Promiscuity means mating with multiple partners in an indiscriminate way, that is, without any selection-based process or quality-based discrimination of mating partners. Contrary to popular belief, promiscuity does not merely mean mating or engaging in sexual activities profusely with different partners. The misuse of the term “promiscuity” in behavioral sciences and evolutionary biology has been pointed out before (Elgar et al. 2013), and the improper use of the term extends to other areas including evolutionary psychology.

The “without choice” qualifier of the term is important because in spite of the fact that males and females mate with multiple partners in most sexually reproducing animal species, in the majority of these species sexual interactions are

governed by mate selection criteria. Thus, applying the strict and correct definition of promiscuity would render very few animals promiscuous indeed. Conversely, if a broader definition of promiscuity was used (e.g., as in “to mate with multiple partners”), then most sexually reproducing species would exhibit promiscuity.

### Promiscuity and Mating Systems

Mating systems are defined by whether individuals associate with one or more sexual partners, and by the sex that engages in multiple sexual interactions with members of the opposite sex. Polyandry occurs when females mate with several males within the same reproductive cycle, polygyny defines the system where males mate with multiple females, and polygynandry takes places when both sexes engage in sexual interactions with multiple partners. These three mating systems are polygamous systems, meaning that either sex or both of them mate with multiple individuals of the opposite sex. They differ from a monogamous mating system in that in such a system each individual of a given sex mates just with one individual of the opposite sex (at least during each discrete reproductive cycle). Promiscuous behavior is possible within polygamous mating systems. It may also occur under social monogamy if individuals engage in copulations outside the social pair-bond (extra-pair copulations).

The terms to define the different mating systems are also used to define behaviors. For instance, polyandry is generally used in the scientific literature to denote the multiple-mates mating behavior of females, even if this behavior occurs outside a formal polyandrous mating system in which females monopolize males. Henceforth, polyandry and polygyny terms will be used in this broad sense, that is, referring to the behavior of multiple mating of females and males respectively.

Interestingly, it has become apparent that many so-called monogamous species are monogamous from a social, but not from a genetic, perspective. The application of modern DNA fingerprinting technology has revealed overwhelming evidence that female multiple mating, the ensuing sperm competition (competition among the sperm from two or more males for the fertilization of a female's ova), and multiple paternity are much more widespread phenomena than it was previously thought (Birkhead and Møller 1998; Birkhead 2000; Barash and Lipton 2001). As an example, the male-female pair bonds established by the great majority (90%) of bird species have proven to be not so tightly bonded. Paternity analyses of broods have uncovered that females in over 70% of these "monogamous" species engage in extrapair copulations (Birkhead 2000; Griffith et al. 2002). In other words, most bird species are socially monogamous but they exhibit genetic polyandry (and genetic polygyny). And this is just a small representation of the extent of multiple mating in nature.

### **Is Multiple Mating Widespread? Is Promiscuity Widespread?**

When it comes to sex, males are often seen as willing, indiscriminate, eager, rampant, sexually demanding, or predisposed for multiple sexual partners. Indeed, in most sexually reproducing species, there is selection on males to mate multiply for well-known reasons rooted in biology, as discussed below. As for females, they have traditionally been seen as reluctant to engage in sexual interactions with multiple partners, and they have

been often defined as acquiescent, coy, or sexually reticent. There is, nonetheless, increasing evidence that this is a simplistic assumption.

Female multiple mating can be found in innumerable species of fish, a great deal of mammal species, many primates including chimps and bonobos, crickets, beetles, numerous fly species, butterflies, damselflies, and many other insect species including members of social insects groups (e.g., some bees, such as honeybees, and several species of ants and wasps), dolphins, most (over 90%) species of birds including socially monogamous species, horseshoes crabs, snails, arachnids, many reptiles, a great deal of amphibians, octopuses and other cephalopods, crustaceans, sharks, and the list continues on and on. By contrast, monogamy (or monandry) is much less frequent. Monogamy occurs in some species of blowflies, several species of social insects including termites, some fish including the majority of seahorses, a handful of species of birds (e.g., geese, some woodpeckers and passerines, swans, kittiwakes, some raptors including owls, etc.), beavers, and a few other species in other groups. Monogamy is the rule in less than 10% of all mammal species, and this includes genetic monogamy and species that form pair-bonds (which are not necessarily sexually monogamous, although unlike birds social monogamy in mammals is generally associated with genetic monogamy) (Lukas and Clutton-Brock 2013). Social monogamy occurs in around 30% of all primate species (e.g., hamadryas baboons), and monogamy has also been documented in some species of bats (6%) and rodents (6%), around 15% of carnivores (notably foxes and coyotes), and less than 3% of ungulates. True monogamy of course occurs less frequently than the percentages shown previously because social monogamy does not always translate into genetic monogamy. Overall, monogamy is not so common or ubiquitous as multiple mating across the animal kingdom.

As for humans, anthropological studies have indicated that strict social monogamy is rare (less than 20% of human cultures). It has been estimated that around 80% of human societies were preferentially polygynous before their contact

with Western cultures. Polyandry as a formal or accepted mating system is exceedingly uncommon, but nonetheless female multiple mating still has some incidence in monogamous or polygynous societies due to extrapair copulations (Simmons et al. 2004; Barash and Lipton 2001; Barash 2016). Female multiple mating is quite common in some cultures (e.g., 70% of Amazonian cultures (Walker et al. 2010)), but genetic analyses indicate that rates of extrapair paternity due to female multiple mating in contemporary Western societies, and through historical times, is low (between 1% and 2%) (Larmuseau et al. 2016). It is important to note, however, that rates of extrapair paternity are a lower limit for rates of female multiple mating since not all matings result in fertilizations (e.g., due to the coitus taking place outside the female's peak fertile period, or to other traditional or modern contraceptive methods).

In summary, most animals exhibit polygamous mating systems or socially monogamous mating systems with varying rates of extra-pair copulations. This does not imply that promiscuity is a ubiquitous behavior. Despite the taxonomic spread of polygamous behavior, research into sexual selection over the last decades has proved that mating preferences are prevalent in all mating systems (Jennions and Petrie 1997). In most primates, as in most other groups, mating preferences for particular males or females are well known. Bonobos are reportedly claimed to behave "promiscuously" to resolve conflicts, and some human groups or individuals are labeled by some people as "promiscuous," but in the majority of cases (perhaps not all) this is the result of a frivolous use of the term.

Mate choice implies that promiscuity *sensu stricto* is infrequent. Some of the best candidates for truly promiscuous animals could be encountered among external fertilizers and in particular broadcast spawners. In these species, multiple individuals of both sexes release their sex cells into the water and so any individual may mate quite indiscriminately with a large number of individuals from the opposite sex. However, recent discoveries are starting to reveal that even in broadcast spawners such as in some species of sea urchins and mussels, reproduction includes a

component of choice at the level of gamete interactions (Evans and Sherman 2013; Evans et al. 2012; Levitan and Ferrell 2006). As for other external fertilizers such as fishes and amphibians mate choice is well documented.

### **Differences Between the Sexes, Sex Roles, Sexual Stereotypes, and Promiscuity**

Typically males and females have different strategies to maximize fitness through sexual reproduction. Many of the disparities between the two sexes in regard to reproduction can be rooted to baseline differences in gamete size between males and females (Trivers 1972). In fact, the size dissimilarity in the sex cells is essentially what defines the sexes: within any given sexually reproducing species the kind of individuals that manufactures relatively smaller (but abundant) gametes are called males, whereas individuals from the sex producing relatively larger (and fewer) gametes are called females. This asymmetry in gamete size (anisogamy) has far-reaching implications for sex roles. For a start, the disparity in gamete size implies that from conception there are differences between the sexes when it comes to the investment they make in the offspring. The female ovum provides the nutrients for the embryo, and females generally provide the environment for embryo development. Males, on the other hand, typically contribute little more than the DNA contained in a minuscule cell. This initial asymmetry in parental investment generally deepens as the offspring develops, especially in vertebrates, with females making a much greater effort protecting or nurturing the embryos and even the young after birth. For instance, pregnancy in a typical mammal lasts several months (e.g., 12 months for horses, 22 months in the case of elephants), and this is followed by lactation. Thus, maternal investment is substantial compared to paternal investment. In other groups, the difference in parental investment between the sexes is not so large but it is still apparent.

The asymmetry in gamete size also means that the sex producing smaller sex cells produces



many more gametes (and at a lower energetic and physiological cost per gamete) than the opposite sex: males typically produce astronomical numbers of gametes, and at a much higher production rates than females. An outcome of this is that males generally compete for access to the limiting resource that allows them to maximize their biological fitness: females, or from a reductionist's point of view, their ova.

Anisogamy and all its direct and indirect implications mean that males can theoretically father hundreds or thousands of offspring with different partners (at the expense of other males). This is well known, and in fact, put into practice, by animal breeders. In contrast, females typically have lower potential reproductive rates (measured in terms of number of offspring) due to them producing fewer gametes (sometimes a fixed low number of ova in a lifetime) and investing a great deal of time and effort into the offspring. In short, sexual differences in gamete size has created reproductive competition among males and asymmetries between the sexes over parental investment and reproduction, with the consequence that male reproductive success is usually limited by the number of mates while female reproductive success is limited by gamete production (Trivers 1972; Bateman 1948; Kokko et al. 2006; Kokko and Jennions 2008; Janicke et al. 2016).

As a consequence of these biological underpinnings, males are expected to be comparatively indiscriminate and females comparatively choosy, and males are expected to be keener than females to engage in multiple matings. Females are expected to maximize their reproductive success with only one or a few matings, and would benefit to a larger extent from careful mate discrimination to ensure their energetically and time-expensive parental efforts go into highly viable or attractive offspring. In humans, for instance, cross-cultural sex differences in sex drive and sociosexuality are well documented, with men typically having more sociosexually unrestricted attitudes and behaviors than women (Schmitt 2005; Lippa 2009). Anisogamy and parental investment disparities are therefore at the core of many morphological, physiological, and behavioral differences between

the sexes in regard to sexual interactions. In the context of the evolutionary drivers of promiscuity, males would thus be expected to benefit more from promiscuous behavior than females, but evidence shows that mate choice underlies, in general, male mating decisions too (Edward and Chapman 2011; Shackelford et al. 2005).

### **Why Do Animals Mate Multiply? And Why Do They Engage in Promiscuous Matings?**

As discussed in the previous section, it is easy to envisage the benefits of multiple mating for males. Sperm is generally produced on a continuous basis, the cost of producing a single sperm, compared to an ovum, is much lower, and male parental investment is low. Thus, males can ultimately maximize fitness (in terms of number of offspring sired) in a more or less proportional way as they increase the number of mating partners. Indeed, polygyny is very common in the animal kingdom. As for females, as a result of anisogamy and a high parental investment they are expected to maximize reproductive success with only one or a few matings. Moreover, the sperm from a single copulation are usually enough to ensure fertilization of the complete set of a female's ova. Finally, mating generally entails costs (for instance, increases in the risk of contracting sexually transmitted diseases), and mating outside the pair bond may entail important costs such as mate desertion in species with biparental care. Consequently, female multiple mating would not be expected to be a common and widespread behavior. Nonetheless, as indicated above polyandry is virtually ubiquitous among sexually reproducing species. Explaining this discrepancy between observation and theory has received considerable attention in recent times (though it is also possible that monandry rather than polyandry is what requires an adaptive explanation; see Kokko and Mappes 2013).

Female mating frequency may be explained, at least in some species, by selection on males to maximize their reproductive success, that is, by sexual conflict leading to higher-than-optimal

mating rates for females (Arnqvist and Rowe 2005). In some other cases, it may be less costly for females to accept copulations than to suffer male sexual harassment (convenience polyandry). In other situations, notably in mammals, female multiple mating may have evolved to create paternity uncertainty so as to deter infanticide. Notwithstanding, from a broader point of view, the evolutionary maintenance of polyandrous behavior is more easily understood when polyandry entails benefits. Indeed, females in some species obtain direct (also known as “material”) benefits from males at copulation. For instance, females can obtain nutrients in the form of food items or substances transferred in the ejaculate during copulation, or by mating multiple females can generate slight confusion regarding paternity and in this way increase the number of partners willing to share care duties, or they may gain access to better territories, or females may mate multiply to ensure fertilization of the ova (fertility insurance).

Regardless of the presence of material benefits, polyandrous females can also obtain genetic benefits from mating multiply. These are benefits that are manifested in the offspring. For instance, females may “trade-up” to obtain good genes for their offspring when a male is considered of superior genetic quality than the female’s previous mate. The traditional “good genes” and “sexy sons” hypotheses hold that females that mate with additional males may increase their fitness indirectly through their offspring because of the inheritance of “good genes” or “attractive genes” (Garcia-Gonzalez and Simmons 2005; Neff and Pitcher 2005).

In addition, one of the most frequently invoked genetic benefits from polyandry in recent years is based on processes that allow females to avoid the negative effects that arise from mating with genetically incompatible males (Neff and Pitcher 2005; Evans et al. 2007). Alternatively, females may engage in copulations with several males to increase the diversity of paternal genotypes in their offspring so that the likelihood that at least some offspring will survive in a changing environment is higher than when offspring genotypes are less diverse (that is, when the females mate monogamously). Finally, females may behave

polyandrously if by mating with multiple males they reduce the risk of having all their offspring sired by a male of low genetic quality (henceforth reducing the risk of potentially losing entire clutches because of low offspring viability). Such risk spreading strategies of the kind “don’t put all your eggs in one basket” are known as bet-hedging polyandry (Garcia-Gonzalez et al. 2015; Yasui and Garcia-Gonzalez 2016).

### **Promiscuity, Direct Benefits, and Bet-Hedging**

Studies have found evidence that females frequently obtain one or several of the benefits above mentioned when they mate with multiple males. However, as it has been pointed out repeatedly in this article, some form or another of female (and male) mate choice is the norm across human and nonhumans, in which case there is no room for talking about promiscuous (indiscriminate) sexual behavior. Nevertheless, promiscuity is compatible with the accrual of direct, and in some circumstances, indirect benefits of mating. Promiscuous behavior is more likely to occur when mating entails direct or material benefits because individuals would obtain the resource (access to food, for instance, in nuptial feeding species) as long as they mate, even though there might be variation in the quality of resources held by potential mates. Indirect benefits are unlikely to explain the evolution of promiscuous behavior in general, because the magnitude of indirect benefits accrued increases following mate quality discrimination and mate choice. For example, high-quality individuals are expected to express traits that indicate their higher reproductive value, and individuals of the opposite sex would be selected to discriminate these signals insofar mating with high-quality individuals gives rise, due to inheritance, to high-quality offspring. Most hypotheses to explain the maintenance of polyandry are based on the existence of mate choice, and the vast majority of indirect (genetic)-based pay-offs from multiple mating are not expected to be responsible for the evolutionary maintenance of



promiscuity, because if individuals can discriminate mate quality they will do so.

There are nonetheless, a few exceptions. For example, if males that attain higher fertilization success via sperm competition sire offspring with higher viability or higher attractiveness, females that mate multiply will increase their fitness simply by facilitating sperm competition among their mates because they will produce attractive, competitive, or viable offspring sired by the most successful mate. This benefit can be obtained in the absence of mate choice, though some sort of female choice either before mating or after mating (e.g., via female-driven paternity biases known collectively as cryptic female choice) is normally in place.

Bet-hedging multiple mating is another hypothesis compatible with promiscuous behavior because a bet-hedging mechanism is based precisely on a lack of sire selection criteria. In some species, or under some circumstances, mate choice is unreliable, imperfect, or absent. In such cases, it may pay to mate multiply and indiscriminately rather than monogamously because, by doing so, individuals may reduce the risk of mating with an unsuitable (low quality, infertile, etc.) partner, or they may reduce the risk of having offspring sired by a single genetic background in a changing and unpredictable environment. In other words, by mating indiscriminately individuals may reduce the consequences of assessment errors when choosing a mate, or they may increase the genetic diversity of their offspring (Garcia-Gonzalez et al. 2015; Yasui and Garcia-Gonzalez 2016). The hypothesis of bet-hedging multiple mating is compatible with promiscuity because it just requires multiple mating, regardless of the phenotypic traits of the potential mates. Empirical tests of this hypothesis are, however, scant.

## Conclusions

It is important not to confuse promiscuity with polyandry, polygyny, or polygynandry (i.e., any form of polygamy). All these terms mean sexual encounters with multiple partners, but

promiscuity is a restrictive term that in reality implies indiscriminate sexual behavior. There cannot be promiscuity without polygamy but there can be polygamy without promiscuity, and in fact this is the most common case in nature. The advent of molecular tools applied to paternity analyses has revealed that multiple paternity within a single brood is commonplace. Multiple mating, either from the perspective of males (polygyny) or females (polyandry), is extremely common in the animal kingdom. In fact, true (genetic) monogamous mating systems have turned out to be exceedingly rare in nature. But, even though we currently know that mating with multiple partners is a common and ubiquitous behavior across animals and occurs with some frequency even in socially monogamous species, promiscuity is extremely rare because when it comes to sexual interactions some form or another of mate choice is the norm. Mate choice is also prevalent in the majority of the diverse range of traditional or modern nonmonogamous relationships or practices exhibited by humans.

## Cross-References

- ▶ [Bateman Gradient](#)
- ▶ [Cryptic Mate Choice](#)
- ▶ [Extra-Pair Copulation](#)
- ▶ [Female Choice](#)
- ▶ [Female Defense Polygyny](#)
- ▶ [Intersexual Selection](#)
- ▶ [Intrasexual Selection](#)
- ▶ [Mating-Systems](#)
- ▶ [Polyandry](#)
- ▶ [Polygamy](#)
- ▶ [Polygyny Threshold Model](#)
- ▶ [Scramble Competition Polygyny](#)
- ▶ [Sexual Attraction](#)
- ▶ [Sexual Selection](#)
- ▶ [Sperm Competition](#)

## References

- Arnqvist, G., & Rowe, L. (2005). *Sexual conflict*. Princeton: Princeton University Press.

- Barash, D. P. (2016). *Out of eden: The surprising consequences of polygamy*. New York: Oxford University Press.
- Barash, D. P., & Lipton, J. E. (2001). *The myth of monogamy*. New York: Henry Holt.
- Bateman, A. J. (1948). Intrasexual selection in *Drosophila*. *Heredity*, 2, 349–368.
- Birkhead, T. R. (2000). *Promiscuity: An evolutionary history of sperm competition and sexual conflict*. London: Faber & Faber.
- Birkhead, T. R., & Møller, A. P. (Eds.). (1998). *Sperm competition and sexual selection*. San Diego: Academic.
- Edward, D. A., & Chapman, T. (2011). The evolution and significance of male mate choice. *Trends in Ecology & Evolution*, 26, 647–654.
- Elgar, M., Jones, T., & McNamara, K. (2013). Promiscuous words. *Frontiers in Zoology*, 10, 66.
- Evans, J. P., & Sherman, C. D. H. (2013). Sexual selection and the evolution of egg-sperm interactions in broadcast-spawning invertebrates. *The Biological Bulletin*, 224, 166–183.
- Evans, J. P., Garcia-Gonzalez, F., & Marshall, D. J. (2007). Sources of genetic and phenotypic variance in fertilization rates and larval traits in a sea urchin. *Evolution*, 61, 2832–2838.
- Evans, J. P., Garcia-Gonzalez, F., Almbro, M., Robinson, O., & Fitzpatrick, J. L. (2012). Assessing the potential for egg chemoattractants to mediate sexual selection in a broadcast spawning marine invertebrate. *Proceedings of the Royal Society B: Biological Sciences*, 279, 2855–2861.
- Garcia-Gonzalez, F., & Simmons, L. W. (2005). The evolution of polyandry: Intrinsic sire effects contribute to embryo viability. *Journal of Evolutionary Biology*, 18, 1097–1103.
- Garcia-Gonzalez, F., Yasui, Y., & Evans, J. P. (2015). Mating portfolios: Bet-hedging, sexual selection and female multiple mating. *Proceedings of the Royal Society of London B*, 282, 20141525.
- Griffith, S. C., Owens, I. P. F., & Thuman, K. A. (2002). Extra pair paternity in birds: A review of interspecific variation and adaptive function. *Molecular Ecology*, 11, 2195–2212.
- Janicke, T., Haderer, I. K., Lajeunesse, M. J., & Anthes, N. (2016). Darwinian sex roles confirmed across the animal kingdom. *Science Advances*, 2, e1500983.
- Jennions, M. D., & Petrie, M. (1997). Variation in mate choice and mating preferences: A review of causes and consequences. *Biological Reviews of the Cambridge Philosophical Society*, 72, 283–327.
- Kokko, H., & Jennions, M. D. (2008). Parental investment, sexual selection and sex ratios. *Journal of Evolutionary Biology*, 21, 919–948.
- Kokko, H., & Mappes, J. (2013). Multiple mating by females is a natural outcome of a null model of mate encounters. *Entomologia Experimentalis et Applicata*, 146, 26–37.
- Kokko, H., Jennions, M. D., & Brooks, R. (2006). Unifying and testing models of sexual selection. *Annual Review of Ecology, Evolution, and Systematics*, 37, 43–66.
- Larmuseau, M. H. D., Matthijs, K., & Wenseleers, T. (2016). Cuckolded fathers rare in human populations. *Trends in Ecology & Evolution*, 31, 327–329.
- Levitan, D. R., & Ferrell, D. L. (2006). Selection on gamete recognition proteins depends on sex, density, and genotype frequency. *Science*, 312, 267–269.
- Lippa, R. A. (2009). Sex differences in sex drive, sociosexuality, and height across 53 nations: Testing evolutionary and social structural theories. *Archives of Sexual Behavior*, 38, 631–651.
- Lukas, D., & Clutton-Brock, T. H. (2013). The evolution of social monogamy in mammals. *Science*, 341, 526–530.
- Neff, B. D., & Pitcher, T. E. (2005). Genetic quality and sexual selection: An integrated framework for good genes and compatible genes. *Molecular Ecology*, 14, 19–38.
- Schmitt, D. P. (2005). Sociosexuality from Argentina to Zimbabwe: A 48-nation study of sex, culture, and strategies of human mating. *Behavioral and Brain Sciences*, 28, 247–311.
- Shackelford, T. K., Schmitt, D. P., & Buss, D. M. (2005). Universal dimensions of human mate preferences. *Personality and Individual Differences*, 39, 447–458.
- Simmons, L. W., Firman, R. C., Rhodes, G., & Peters, M. (2004). Human sperm competition: Testis size, sperm production and rates of extrapair copulations. *Animal Behaviour*, 68, 297–302.
- Trivers, R. L. (1972). Parental investment and sexual selection. In R. Campbell (Ed.), *Sexual selection and the descent of man* (pp. 136–179). London: Heinemann.
- Walker, R. S., Flinn, M. V., & Hill, K. R. (2010). Evolutionary history of partible paternity in lowland South America. *Proceedings of the National Academy of Sciences*, 107, 19195–19200.
- Yasui, Y., & Garcia-Gonzalez, F. (2016). Bet-hedging as a mechanism for the evolution of polyandry, revisited. *Evolution*, 70, 385–397.

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## Thyroid and Adrenal Glands

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### Definition

**Thyroid gland:** a collection of follicular cells surrounding a colloid space that concentrate dietary iodine and produce the thyroid hormones thyroxine (T4) and triiodothyronine (T3). Individual follicles may or may not be organized into a larger structure depending upon taxa.

**Adrenal gland:** endocrine gland located next to the kidney responsible for production of a number of hormones including the glucocorticoids as well as the catecholamines.

### Thyroid Gland

#### Introduction

The thyroid gland and its products thyroxine (T4) and triiodothyronine (T3) are present across vertebrate taxa. As with all endocrine glands the thyroid is ductless and highly vascularized and thyroid hormones are excreted directly into circulation upon secretion. The thyroid gland is unique

among the endocrine glands because of its dependence upon dietary iodine for hormone production and its ability to concentrate and store dietary iodine.

#### Anatomy

Though functionally highly conserved, the location and gross anatomy of the thyroid gland varies across vertebrate taxa. Generally in most taxa, the gland(s) are located within the neck region, though the precise location varies. The exception to this rule is the Echidna in which the thyroid is present as a pair of unattached glands located in the thorax. In cyclostomes and most teleosts, the gland is disorganized with follicles scattered in the region of the pharynx (Gorbman et al. 1983). In frogs, amphibians, mammals, and birds, the gland exists as a two separate lobes that occur bilaterally. In mammals and humans, in particular, it is composed of two distinct lobes connected by an isthmus, located in the anterior portion of the neck lying on the trachea between vertebrae C5 and T1 (Gorbman et al. 1983). With the exception of the cyclostomes and teleosts in which the gland is disorganized, the thyroid gland, regardless of gross anatomy, is comprised of small spherical follicles. These follicles are formed by a layer of epithelial follicular cells surrounding the follicular lumen (a.k.a. follicular or colloid space), an open space that is filled with fluid-like colloid. Regardless of organizational

structure, the resulting thyroid follicles are highly vascularized to support both iodine uptake and secretion of its hormonal products.

### Iodine Uptake

Production of thyroid hormones begins with the active uptake of iodine by the thyroid gland. Concentration of iodine within the gland against its concentration gradient is accomplished by active transport of iodine by and  $\text{Na}^+/\text{I}$  symporter. The end result of this active transport is the concentration of iodine within the colloid space of the follicles.

### Production of Thyroid Hormones

Thyroid hormone production begins with the synthesis of thyroglobulin, an approximately 660-kDa glycoprotein homodimer, in the endoplasmic reticulum of follicular cells. Thyroglobulin is stored within the follicular lumen, where the enzyme thyroid peroxidase (TPO) catalyzes the iodination of the tyrosine residues to form either mono-iodinated or di-iodinated tyrosine residues. Subsequently, coupling of iodinated tyrosine residues results in the formation of T3 and T4 residues. The iodinated thyroglobulin is stored within the follicular lumen until needed. In response to central signaling from the brain, iodinated thyroglobulin molecules are endocytosed into the follicular cells and the iodothyronine residues are cleaved to create T4 and T3, which are then secreted into circulation. Typically, T4 forms the vast majority of the hormone secreted into circulation while T3 comprises only a small fraction.

### Central Control of Thyroid Hormone Production and Signaling

Thyroid hormone production and secretion is controlled by the hypothalamic–pituitary–thyroid (HPT) axis. Neural inputs of both environmental and internal stimuli are integrated in the brain and cause stimulation of the parvocellular neurons in the paraventricular nucleus of the hypothalamus triggering the release of thyrotropin-releasing hormone (TRH) that acts on thyrotroph cells in the anterior pituitary to cause the release of thyroid-stimulating hormone (TSH). After entering the blood stream, TSH binds to the G-

protein–coupled receptors of the follicular cells, triggering the release of thyroid hormones from the follicular cells, and stimulates increased iodine uptake and thyroid hormone synthesis by the gland. The activity of the HPT axis is controlled through classic negative feedback mechanism, in which circulating thyroid hormones bind to receptors in parvocellular neurons in the arcuate nucleus of the hypothalamus and the thyrotroph cells in the anterior pituitary gland to reduce the activity of these two points in the hormonal axis.

### Carrier Proteins

As with most hormonal systems, thyroid hormones are subject to multiple levels of regulation beyond central control of production and release. Following secretion from the thyroid gland, circulating hormones become bound to carrier proteins, which form the bulk of the hormone in circulation (Yen 2001). There are three major carrier proteins for thyroid hormones: thyroid-binding globulin, transthyretin (TTR; previously TBPA), and albumin (Larsson et al. 1985). TTR is of particular interest as it is found not only in circulation, but expression has been identified in other tissues including the liver and choroid plexus of birds (Power et al. 2000). Binding to carrier proteins protects bound hormone from enzymatic degradation and clearance, but also limits its ability to enter cells and bind to target receptors, thus controlling in part cellular exposure to bioactive hormone.

### Membrane Transporters

Until recently, dogma held that thyroid hormones were able to enter target cells via passive diffusion across the plasma membrane (Robbins and Rall 1960). However, recent work has uncovered a large array of membrane transporters that actively transport thyroid hormones across the plasma membrane. At present, over 21 different transport proteins have been identified with varying degrees of specificity for the iodothyronine derivatives: including organic anion-transporting polypeptide transporters (e.g., OATP1C1), monocarboxylate transporter family members MCT8 & MCT10, and L-type amino acid transporters (reviewed in Visser et al. 2011). While these

transporters are beginning to be characterized in mammalian systems, little is known about their distribution, functionality, or expression patterns in most other taxa and broad-scale comparative work is completely lacking. However, the need for membrane transport of thyroid hormones allows for a wide array of potential regulatory schema. Evidence has emerged from multiple species identifying expression of transport proteins in the brains of rats and birds, particularly in the blood–brain barrier. Expression of transporters in the blood–brain barrier with differential specificity for T3 versus T4 may be critical for regulating whole brain exposure to thyroid signaling, particularly in conjunction with deiodinase regulatory activity.

### Regulatory Enzymes

Though T4 is the major product of the thyroid gland in circulation, receptor binding studies have shown that thyroid hormone receptors (THR) have significantly higher affinity for T3 as compared to T4; thus, T3 has long been considered the bioactive form of the hormone with T4 often being considered a precursor hormone. The conversion of T4 to T3 is under the control of the second major level of thyroid hormone regulation, the deiodinase enzyme system. This system is comprised of three enzymes: deiodinases type I, II, and III (DIO1, DIO2, DIO3), which function by removing iodine from different positions. All three deiodinases require selenium for functional catalytic activity; thus, either dietary deficiency or defects in synthesis of selenoproteins results in various defects in deiodinase activity and negative feedback control of the HPT axis. Despite these basic similarities, these three enzymes differ in their distribution and the reactions they catalyze. Found primarily in the liver, kidney, and thyroid gland itself, DIO1 is capable of deiodinating both the inner and outer rings of thyroid hormone molecules, thus catalyzing both the conversion of T4 to the more potent T3 and also the inactivation of T4 by conversion to reverse T3 (rT3) or inactivating T3 via conversion to T2. DIO1 is considered primarily to serve a systemic regulatory role, maintaining the appropriate T3/T4 ratio in the plasma and scavenging iodine from sulfated

hormone for clearance in either bile or urine. DIO2 on the other hand is most abundant in the brain, pituitary, thyroid, brown adipose tissue (BAT), and skeletal muscles. DIO2 acts as an outer ring deiodinase catalyzing the conversion of T4 to T3; thus, it is considered the primary activating enzyme. In contrast, DIO3 is primarily responsible for inactivation of various forms of thyroid hormone via inner ring deiodination. DIO3 is abundant in skin and vascular tissue, but is also found in the brain, pituitary, and other tissues. DIO3 also plays a key role in the placenta in protecting the developing fetus from excessive maternal thyroid hormones that might interfere with development. Together DIO2 and DIO3 act locally to control cellular exposure to T3 and thus thyroid signaling. All three deiodinases have been shown to vary both over the course of ontogeny but also seasonally, particularly in seasonally breeding animals.

### Receptors

Ultimately, thyroid hormone signaling is mediated by the binding of predominately T3 to nuclear receptors that regulate gene transcription. There are three isoforms of THR: THR $\alpha$ , THR $\beta$ , and THR $\beta$ 2, which form heterodimers with retinoid X receptors ( $\alpha$  and  $\gamma$  isoforms) to bind thyroid-response elements in the DNA. As with many nuclear receptors, the hormone binds to the receptor, which then translocates to the nucleus and binds to a thyroid-response element activating transcription of the target gene. However, evidence has emerged suggesting that unbound receptor complexes may bind to response elements independent of the hormone. In these cases, the unbound receptor may either suppress or activate transcription, with ligand binding leading to the opposite effect (Mullur et al. 2014). Further complicating the picture is the interaction of thyroid receptors with multiple corepressor and coactivator systems, which respond to a variety of signals including, but not limited to, nutritional and adrenergic signals. In addition to the traditional genomic receptors, non-genomic thyroid signaling pathways have been found by both in vitro and in vivo studies. In particular, the transmembrane protein integrin

$\alpha\text{v}\beta\text{3}$  has two thyroid-binding sites, one that preferentially binds T3 and the other T4, with differential output depending upon the ligand that is bound. Thyroid hormones have also been identified acting in multiple phosphorylation pathways.

### **Actions of Thyroid Hormones Across Vertebrates**

Thyroid hormones have been long considered to be a “slow” hormone often acting in a permissive manner. Traditionally, they are most closely associated with ontogenetic development, metamorphosis, general growth, and regulation of metabolic function. Disruption of proper thyroid function is also associated with a number of disease processes across vertebrate taxa.

Thyroid hormone action has been tied to development of the brain, sensory, skeletal, muscle, and other organ systems. These effects are mediated not only through genomic receptors altering gene expression, but also through modulation of kinase signaling pathways. In keeping with regulation of developmental programs, thyroid hormone signaling has been established as the sole signal necessary to trigger the metamorphosis from tadpole to adult in amphibians.

Apart from their major role in development and metamorphic processes, thyroid hormones are major regulators of metabolism. Thyroid signaling has been tied to regulation of basal metabolic rate, cholesterol synthesis, lipolysis, gluconeogenesis, cellular ion gradients, and insulin production. These actions are mediated through both genomic and nongenomic thyroid action involving numerous corepressor, coactivators, and varying receptor isoforms, and cross talk with other regulatory systems that are beyond the scope of this work, but see Mullur et al. (2014) for in-depth review.

Thyroid hormones are also tied to adaptive thermogenesis, as is supported by the observation that hypothyroid humans and animals readily develop hypothermia in response to cold exposure, while hyperthyroid individuals typically maintain elevated body temperature. Adaptive nonshivering thermogenesis in rodent models has been tied to BAT and specifically expression

of uncoupling protein (UCP) 1, which is locally regulated by T3 following conversion from T4 by DIO2.

### **Thyroid Hormones as Regulators of Seasonality**

Thyroid hormones have recently emerged as potent regulators of seasonality. In particular, thyroid hormones have been identified as key regulators of seasonal breeding in both birds and mammals (Dawson 2002). Upregulation of TSH production in the pars tuberalis of the hypothalamus in response to daylength cues acting through TSH leads to increased DIO2 expression within the hypothalamic tanycytes, resulting in local T3 signaling that triggers the release of gonadotropin-releasing hormone (GnRH) which starts a well-characterized hormonal cascade, responsible for the regulation of breeding (Yoshimura 2010). Thyroid hormones have also been shown to be necessary for the expression of vernal migration (Pérez et al. 2016) and molt (Voitkevich 1966) in birds, but molecular mechanisms of action remain largely unknown for these and other seasonal processes.

### **Conclusion**

Highly conserved and pleiotropic in their function, the thyroid gland and its products are critical regulators of a wide array of processes, with more continuing to be identified. Despite a robust understanding of their molecular actions, particularly with regards to development, metabolism, thermogenesis, and disease processes in humans and other mammalian systems, much less is known regarding these processes in nonmodel systems.

## **Adrenal Gland: Glucocorticoids**

### **Introduction**

The adrenal gland is one of the major endocrine glands located on the posterior wall of the abdominal cavity and sites on the superior aspect of the kidney as its name would suggest. The adrenal gland contains steroidogenic enzymes responsible



for the synthesis of numerous hormones including aldosterone, dehydroepiandrosterone (DHEA), cortisol, and corticosterone. Furthermore, they are also responsible for the synthesis of the catecholamines, epinephrine, and adrenaline as well as small quantities of norepinephrine and noradrenaline.

### Anatomy

The anatomy of the adrenal gland varies across taxa. Mammals typically have an adrenal gland that is composed of an outer cortex composed of three distinct layers with an inner medullary region. The three unique regions of the cortex moving from the outer most to inner most layers include zona glomerulosa, fasciculata, and reticularis. In other taxa such as birds, the same level of organization is not present and cells of the cortex are mixed with medullary cells. In fish, an organized adrenal is almost completely absent and instead adrenal cells are dispersed throughout the kidney tissue. Despite the lack of adrenal anatomical homology across taxa, the cells responsible for producing each of the mineralocorticoids, glucocorticoids, and sex steroids are present in all taxa.

Each of three zones expresses a unique set of steroidogenic enzymes that are responsible for the production of various steroids. The zona glomerulosa produces mineralocorticoids such as aldosterone which plays a critical role in maintaining water balance by controlling the expression of sodium and potassium channels in the kidney. The zona reticularis produces DHEA, a weak androgen that is thought to regulate aggression during the nonbreeding season in many species. Finally, the zona fasciculata contains steroidogenic enzymes that control the production of glucocorticoids, cortisol, and corticosterone, which regulate the stress response. Additionally, the medullary region of the adrenal gland expresses chromaffin cells which are aptly named for the affinity for chromaffin dye and are responsible for the production of catecholamines, epinephrine/adrenaline, although norepinephrine/noradrenaline are also produced in small quantities. Epinephrine is released in response to the activation of the autonomic nervous system

and has wide effects including increased heart rate, pupil dilation, slowed intestinal motility, etc. However, as this text is focused on behavior and cognition, the emphasis for the remainder of this section will be on the production of glucocorticoids and their major actions.

### Glucocorticoids

The major glucocorticoid secreted by the adrenal gland can either be corticosterone or cortisol depending on the species although the modes of action are identical. Corticosterone is the primary glucocorticoid in birds, rodents, and amphibians while cortisol is the primary glucocorticoid in primates, pinnepeds, fish, and whales. The difference in production is dependent upon the presence and abundance of key steroidogenic enzymes within the adrenal glands. As with all steroid hormones, glucocorticoids are derived from cholesterol either of dietary origin or synthesized *de novo* within cells. Cholesterol molecules are largely stored in lipid droplets within the steroidogenic cells of the adrenals. Final cortisol synthesis occurs in the zona fasciculata, while corticosterone is synthesized in the zona glomerulosa. In both cases, the steroidogenic enzymes responsible are found both in the intracellular spaces and within the mitochondria, where the final steps of synthesis occur. For both glucocorticoids, the final steps in synthesis involve conversion by 21-hydroxylase to an 11-deoxy form (either 11-deoxycortisol or 11-deoxycorticosterone) from either progesterone (corticosterone) or 17 $\alpha$ -hydroxyprogesterone. The 11-deoxycort is then converted by 11 $\beta$ -hydroxylase into its final form (Salway 1999). Since the final steroid products are lipophilic, they cannot be synthesized and stored like peptide hormones, but rather are immediately diffused into circulation.

### Central Regulation

As with thyroid hormones, production of glucocorticoids is centrally regulated by several key hormonal signaling cascades. Glucocorticoid synthesis is controlled by the hypothalamic–pituitary–adrenal (HPA) axis, which receives input on both metabolic and

psychological stressors. The regulation of the HPA axis begins in the brain at the level of the hypothalamus as it integrates cognitive information from higher cortical regions such as amygdala and hippocampus, which provide information on feelings of fear, anger, stress, etc. and information on metabolic status from other nuclei within the hypothalamus itself. Metabolic and psychological signals are integrated by the paraventricular nucleus of the hypothalamus, regulating the release of neuropeptide hormones. For most mammalian species, the PVN releases corticotropin-releasing hormone (CRH; 41 aa) and arginine vasopressin (AVP; 9 aa) into the portal vasculature of the median eminence where they travel to the anterior pituitary gland to interact with CRH and AVP receptors located on corticotrope cells. In birds, CRH is released in conjunction with arginine vasotocin (AVT) instead of AVP. Activation of corticotrope cells leads to the release of adrenocorticotrophic hormone (ACTH; 39 aa), which travels through the blood stream to the adrenal gland where it binds to melanocortin receptors primarily in the zona fasciculata. Activation of these receptors leads to the increased activity of steroidogenic acute regulatory (STAR) enzyme and side-chain cleavage enzyme activity, which are the two rate-limiting enzymes in steroid production. The activation of the HPA has a very weak stimulatory effect on the synthesis of sex steroids and mineralocorticoids. Synthesis of mineralocorticoids, such as aldosterone, is primarily under the control of the renin-angiotensin system.

### Carrier Proteins

Since steroid hormones are hydrophobic, they need to be transported in the blood and bound to carrier proteins. Carrier proteins allow for rapid transport of steroids through the blood stream. Cleavage by serpinase enzymes at the target tissues allow for rapid release of the hormone. The diversity of these proteins varies by species with many mammalian, reptilian, and amphibian species having sex steroid-specific binding proteins and multiple glucocorticoid-binding proteins, while birds have just a single glucocorticoid-binding globulin. Carrier proteins bind their preferred

steroids with a high affinity but are considered low capacity when compared to the ability of other plasma proteins to bind steroids such as albumin. The presence of carrier proteins leads to the classification of hormones that are bound by the carrier protein which represent a majority of the steroid in circulation and steroids that are not bound by the carrier protein which are called free. Much debate has focused on whether bound, free, or bound and free are responsible for the biological action of the steroid. Many theories have been put forth on the functional role of carrier proteins that is only starting to fully be understood with modern molecular techniques. The evidence today would suggest that glucocorticoid's ability to produce a biological response is mediated by both steroids that are bound by transport proteins and ones that are free in the plasma as well.

### Regulatory Enzymes

In addition to the production of steroid hormones by the adrenal glands and other tissue which perform *de novo* synthesis, steroid levels at the level of the tissue can also be rapidly modified. One of the major enzymes involved in corticosterone signaling is the enzyme 11 $\beta$ -hydroxysteroid dehydrogenase that can be found in two isoforms. 11 $\beta$ -hydroxysteroid dehydrogenases convert glucocorticoids into less active metabolites (11 $\beta$ -HSD2), while 11 $\beta$ -HSD1 performs the reverse reaction (Seckl and Chapman 1997). Expression of these enzymes allows for rapid regulation at the target tissue which can either increase or decrease the amount of steroids that are available to interact with either membrane-bound or nuclear receptors. Little is known about seasonal expression of these enzymes, but they play a critical role in regulating how much glucocorticoid actually encounters intracellular receptors in a cell (Seckl and Chapman 1997).

### Receptors

In birds and mammals, there are two intracellular genomic receptors that bind to corticosterone and less well studied membrane-bound receptors (Breuner and Orchinik 2009). The genomic mineralocorticoid receptor (MR, Type I) has a tenfold

higher binding affinity for corticosterone than the genomic glucocorticoid receptor (GR, Type II). As for the membrane-bound receptors, genomic MR can be targeted for the cell membrane where it acts as a membrane-bound receptor and there is also a unique membrane-bound glucocorticoid receptor (Joëls et al. 2008). Insertion of the nuclear MR in the membrane results in a tenfold reduction in receptor affinity for glucocorticoids and thus has similar binding characteristics as GR. Membrane-bound receptors act through second messenger systems to promote rapid changes in cell activity. This difference in binding affinity is thought to create a two-tier system for responding to basal and stress-induced levels of corticosterone with negative feedback mediated by receptors according to ligand affinity (de Kloet et al. 1998). Nuclear membranes can be found in the cytosol bound to heat-shock proteins (HSP). Once the glucocorticoids bind to the receptor, HSP dissociate which allows for translocation into the nucleus of the cell. Both genomic receptors are transcriptional factors with a zinc finger motif that bind to their respective glucocorticoid-responsive elements to influence gene transcription (de Kloet et al. 1998).

### Major Roles

Glucocorticoids are named after their first discovered function, which is to raise plasma levels of glucose by increasing gluconeogenesis. In addition, glucocorticoid hormones have been termed stress hormones because of their role in helping animals cope with stressful events and are activated at the same time as the flight or fight response by the autonomic nervous system (de Kloet et al. 1998). Physiologists tend to study circulating levels during basal conditions which are thought to reflect levels in an undisturbed animal. At basal levels, glucocorticoids are largely thought to be involved in regulating metabolism. Physiologists are also interested in how glucocorticoid concentrations change in response to stressors such as handling, captivity, predation, weather events, etc., which reflect concentrations that are much higher than basal concentrations and are often called stress-induced or peak glucocorticoids. Stress-induced levels of

glucocorticoids are thought to play a different role than baseline levels helping the animal cope with the stressor by inducing drastic changes in physiology and behavior (Krause et al. 2016).

The role of hypothalamic–pituitary–adrenal (HPA) axis is to modify vertebrate behavior and physiology in response to unpredictable events (Sapolsky et al. 2000). Physiological changes must occur for an individual to survive in conditions that are beyond those normally experienced (Boonstra 2004; Wingfield et al. 2015). Glucocorticoids are often thought to regulate overall energetic expenditures during stressors by reducing the activity of certain systems such as digestion, reproduction, etc., so that greater energy can be devoted toward systems required for immediate survival such as the skeletal muscle system. Thus, scientists have proposed that the activity of the HPA axis is linked with making important life history tradeoff decisions. For instance, when environmental conditions become sufficiently harsh that reproduction must be abandoned in order to save one's self at the cost of losing both one's self and their offspring, either baseline or stress-induced corticosterone levels are elevated (Krause et al. 2016). The actions of glucocorticoids on life history decisions are likely best studied in birds because of the ease at which parents and offspring can be monitored to see when critical points are reached that necessitate nest abandonment. In many bird species, there appears to be a threshold at which corticosterone levels will trigger nest abandonment. Slight increases can be beneficial and have been shown to be positively correlated with reproductive success. The thought being that parents that work harder to provision their offspring likely have slightly higher corticosterone levels in order to help fuel metabolism (Ouyang et al. 2013).

During periods of stress and negative energy balance, rising corticosterone concentrations have been linked with protein catabolism (Fokidis et al. 2012), lipid mobilization (Landys et al. 2004), escape behavior (Breuner and Hahn 2003), hyperactivity in cages (Lynn et al. 2003), suppression of reproduction (Calisi et al. 2008), increased feeding activity (Astheimer et al. 1992; Fokidis et al. 2012), predator awareness

(Jones et al. 2015), enhanced memory formation and consolidation, and enhanced immune function (Sapolsky et al. 2000), all of which are thought to promote survival. Each of these examples is a testament to how many systems can be affected by the actions of corticosterone.

Prolonged stressors can lead to situations in which animals are chronically stressed. On the acute, time scale activation of the HPA axis is beneficial for the organism and promotes changes in physiology and behavior that are necessary for survival. However, prolonged activation of the system, as observed with chronic stress, can have pathological consequences such as reduced fecundity, mass loss, reduced immune function, redistribution of fat deposits, etc. Chronic stress often results in unusual and inconsistent patterns of HPA axis function from changes in baseline corticosterone concentrations, changes in the stress profile, and finally changes in the density of MR and GR receptors in the brain.

## References

- Astheimer, L. B., Buttemer, W. A., & Wingfield, J. C. (1992). Interactions of corticosterone with feeding, activity and metabolism in passerine birds. *Ornis Scandinavica*, 23(3), 355–365.
- Boonstra, R. (2004). Coping with changing northern environments: The role of the stress axis in birds and mammals. *Integrative and Comparative Biology*, 44, 95–108.
- Breuner, C. W., & Hahn, T. P. (2003). Integrating stress physiology, environmental change, and behavior in free-living sparrows. *Hormones and Behavior*, 43(1), 115–123.
- Breuner, C. W., & Orchinik, M. (2009). Pharmacological characterization of intracellular, membrane, and plasma binding sites for corticosterone in house sparrows. *General and Comparative Endocrinology*, 163(1–2), 214–224.
- Calisi, R. M., Rizzo, N. O., & Bentley, G. E. (2008). Seasonal differences in hypothalamic EGR-1 and GnIH expression following capture-handling stress in house sparrows (*Passer domesticus*). *General and Comparative Endocrinology*, 157(3), 283–287.
- Dawson, A. (2002). Photoperiodic control of the annual cycle in birds and comparison with mammals. *Ardea*, 90(3 Special Issue), 355–367.
- de Kloet, E. R., Vreugdenhil, E., Oitzl, M. S., & Joëls, M. (1998). Brain corticosteroid receptor balance in health and disease. *Endocrine Reviews*, 19(3), 269–301.
- Fokidis, H. B., des Rozières, M. B., Sparr, R., Rogowski, C., Sweazea, K., & Deviche, P. (2012). Unpredictable food availability induces metabolic and hormonal changes independent of food intake in a sedentary songbird. *Journal of Experimental Biology*, 215(16), 2920–2930.
- Gorbman, A., Dickhoff, W. W., Vigna, S. R., Clark, N. B., & Ralph, C. L. (1983). *Comparative endocrinology*. New York: Wiley.
- Joëls, M., Karst, H., DeRijk, R., & de Kloet, E. R. (2008). The coming out of the brain mineralocorticoid receptor. *Trends in Neurosciences*, 31(1), 1–7.
- Jones, B. C., Smith, A. D., Bebus, S. E., & Schoech, S. J. (2015). Two seconds is all it takes: European starlings (*Sturnus vulgaris*) increase levels of circulating glucocorticoids after witnessing a very brief raptor attack. *Hormones and Behavior*, 78, 72–78.
- Krause, J. S., Pérez, J. H., Chmura, H. E., Meddle, S. L., Hunt, K. E., Gough, L., Boelman, N., & Wingfield, J. C. (2016). The stress response is attenuated during inclement weather in parental, but not in pre-parental, Lapland longspurs (*Calcarius lapponicus*) breeding in the low Arctic. *Hormones and Behavior*, 83, 68–74.
- Landys, M. M., Piersma, T., Ramenofsky, M., & Wingfield, J. C. (2004). Role of the low-affinity glucocorticoid receptor in the regulation of behavior and energy metabolism in the migratory red knot *Calidris canutus islandica*. *Physiological and Biochemical Zoology*, 77(4), 658–668.
- Larsson, M., Pettersson, T., & Carlström, A. (1985). Thyroid hormone binding in serum of 15 vertebrate species: Isolation of thyroxine-binding globulin and prealbumin analogs. *General and Comparative Endocrinology*, 58(3), 360–375.
- Lynn, S. E., Breuner, C. W., & Wingfield, J. C. (2003). Short-term fasting affects locomotor activity, corticosterone, and corticosterone binding globulin in a migratory songbird. *Hormones and Behavior*, 43(1), 150–157.
- Mullur, R., Liu, Y.-Y., & Brent, G. A. (2014). Thyroid hormone regulation of metabolism. *Physiological Reviews*, 94(2), 355–382.
- Ouyang, J. Q., Muturi, M., Quetting, M., & Hau, M. (2013). Small increases in corticosterone before the breeding season increase parental investment but not fitness in a wild passerine bird. *Hormones and Behavior*, 63(5), 776–781.
- Pérez, J. H., Furlow, J. D., Wingfield, J. C., & Ramenofsky, M. (2016). Regulation of vernal migration in Gambel's white-crowned sparrows: Role of thyroxine and triiodothyronine. *Hormones and Behavior*, 84, 50–56.
- Power, D. M., Elias, N. P., Richardson, S. J., Mendes, J., Soares, C. M., & Santos, C. R. A. (2000). Evolution of the thyroid hormone-binding protein, transthyretin. *General and Comparative Endocrinology*, 119, 241–255.
- Robbins, J., & Rall, J. (1960). Proteins associated with the thyroid hormones. *Physiological Reviews*, 40, 415–489.

- Salway, J. G. (1999). *Metabolism at a glance*. Oxford: Blackwell Science.
- Sapolsky, R. M., Romero, L. M., & Munck, A. U. (2000). How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions. *Endocrine Reviews*, *21*(1), 55–89.
- Seckl, J. R., & Chapman, K. E. (1997). Medical and physiological aspects of the 11beta-hydroxysteroid dehydrogenase system. *European Journal of Biochemistry/FEBS*, *249*(2), 361–364.
- Visser, W. E., Friesema, E. C. H., & Visser, T. J. (2011). Minireview: Thyroid hormone transporters: The knowns and the unknowns. *Molecular Endocrinology*, *25*(1), 1–14.
- Voitkevich, A. A. (1966). *The feathers and plumage of birds*. London: Sidgwick & Jackson.
- Wingfield, J., Krause, J., Perez, J., Chmura, H., Németh, Z., Word, K., Calisi, R., Meddle, S. (2015). A mechanistic approach to understanding range shifts in a changing world: What makes a pioneer? *General and Comparative Endocrinology*, *222*, 44–53.
- Yen, P. M. (2001). Physiological and molecular basis of thyroid hormone action. *Physiological Reviews*, *81*(3), 1097–1142.
- Yoshimura, T. (2010). Neuroendocrine mechanism of seasonal reproduction in birds and mammals. *Animal Science Journal*, *81*(4), 403–410.

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## Laterality (Handedness)

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### Synonyms

[Behavioral lateralization](#); [Cerebral asymmetry](#);  
[Hand preference](#)

### Definitions

*Laterality* is where one hemisphere exerts dominance over the other in the control of a particular behavior or function.

*Handedness* may be defined as the tendency to use one forelimb preferentially for a specific task.

### Introduction

In 1861, Paul Broca published the first paper that tied a cerebral asymmetry to a specific behavioral function and localized that function to a particular hemisphere of the human brain. By finding that “Broca’s area” in the left hemisphere controlled the ability to speak, a new area of research was initiated. Laterality is the condition wherein a function is controlled by a specific hemisphere of the brain. In Broca’s treatise, language is “lateralized” to the left hemisphere. Human

primates (*Homo sapiens*) have an unusually high population-level right-hand preference that is displayed across cultures (Hecaen and Ajuriaguerra 1964). This right-hand preference is highly correlated among fine manipulative tasks and tasks associated with hand/eye coordination (Seltzer et al. 1990). Many have hypothesized that speech and manipulative ability involve similar types of motor control whereby individual systems of muscles must be timed to excite and inhibit in a sequential manner (Kimura 1976). Understanding the progression of the relationship between motor control systems that serve manipulation and speech may best be achieved through the study of nonhuman primates. This is because they have more specialized neuroanatomy for motor control of the forelimb (Nudo and Masterton 1990; Nudo et al. 1995) and a morphological forelimb structure that permits greater mobility of the fingers (Napier 1980).

The primate hand and brain have undergone changes in structure that allow for enhanced neuromuscular control of the fingers. The progression from prehensile grasping to individuated finger movements is exhibited to varying degrees among primate species and offers an opportunity to examine how the hand may have led the brain in evolution (Preuschoft and Chivers 1993). A related aspect of hand/brain function is related to manual specialization wherein a particular hand is favored over the other for a particular task. *Handedness* may be defined as the tendency to use one forelimb preferentially for a specific task.



The way in which the tendency is determined has involved using statistics to evaluate whether left- or right-hand usage has occurred significantly more than chance. The statistical procedures have generally utilized either standard scores (z-scores) or a handedness index (HI) (for a review of these approaches, see Hopkins 1999).

Handedness is generally seen to reflect an underlying cerebral lateralization or hemispheric specialization wherein the right hemisphere controls functions on the left side and the left hemisphere controls the right (Hopkins 2007). The lateralization or specialization of each hemisphere may represent evolutionary trends as hypothesized by MacNeilage (2007). This progression mirrors the evolution of forelimb manipulative abilities and may also be related to the species feeding niche specializations. MacNeilage et al. (1987) believe that the rudimentary form of lateralization that is still evident in Prosimians and specifically in insectivorous vertical clingers and leapers involved a right hemisphere (left-hand) specialization for insect capture and a left hemisphere (right-hand) specialization for postural support. With speciation and pressure to expand the insectivore niche to include fruit or foods that require increased manipulative skill to remove the edible portions from the matrix in which they are embedded, a change in manual specialization was required. This change involved the left hemisphere (right hand) changing its specialization from postural support to manipulative skill and associated refinement in individuated finger movements and a precision type of grip. MacNeilage et al. (1987) proposed that this progression may be seen in the way in which anthropoid primates and especially old-world primates use their hands to forage for embedded food resources where the left hand retains its prehensile grasp on the food item and the right hand manipulates the husk or peel to reach the edible portions. Although there is good amount of evidence to support these ideas in the prosimian literature (for reviews see Ward et al. 1993; Watson and Hanbury 2007), the progression toward a right-hand manual specialization hypothesized among anthropoids is less consistent but becomes somewhat more consistent when hand preferences are

interpreted in light of the behavioral task and when body posture is also taken into account (MacNeilage 2007).

Although many researchers support an evolutionary approach to the study of lateralization that predicts a continuity in behaviors tied to cerebral asymmetries within the order Primates, there are those who believe the human language represents a unique ability that differentiates *Homo sapiens* from the rest of the animal kingdom (Corballis 1991). It is proposed that the lateralization of speech seen in human language helps to magnify the associated right-handedness seen in the human population. Because a similar *population-level* trend is not seen in other primate species, this is taken as evidence against the gradual evolution of primate handedness. McGrew and Marchant (1997) performed a meta-analysis on 241 published primate laterality studies and found that only captive chimpanzees displayed some degree of right-handedness that would begin to approximate the human condition. They also did not find any appreciable phyletic progression toward this right preference and argued against the validity of handedness data derived from captive populations.

Many of the inconsistencies noted in the old-world monkey literature are due to differences in the tasks used to evaluate handedness and whether postures were accounted for. For example, measures of hand preference have generally enlisted a simple food-reaching task that involved the primate reaching for food and then eating it. While this may provide a measure of lateralization related to simple food reaching, it may be the case that a different hand is used to hold the food while it is being consumed or perhaps the feeding task is bimanual with one hand holding food and the other extracting edible portions from the peel. In this sense it is sometimes difficult to assess handedness because the hands are perhaps being used for different elements of the feeding task. It has been demonstrated that factors such as reach posture (bipedal vs. quadrupedal), substrate (arboreal vs. terrestrial), type of grasp (prehensile vs. precision, bimanual vs. unimanual), food type, and size do influence the direction and strength of handedness

(Meguerditchian et al. 2013). It is only through careful analyses utilizing multiple measures of hand use that we may reveal factors that may have promoted early forms of lateral preference. It could be the case that the gradualist approach hypothesized in the postural origin theory may be too general with respect to the transition to right-handedness in Anthropoid primates and that several species-specific factors may converge and result in a population-level trend.

## Cerebral Asymmetry

The search for anatomical asymmetries that are indicative of cerebral lateralization has focused on morphological or electrophysiological differences between the hemispheres. The finding that great apes and humans share a larger area 44 (homologue to Broca's area) in the left hemisphere when compared with the right indicates that at least in chimpanzees and gorillas, a structural lateralization similar to the human condition exists (Cantalupo and Hopkins 2001). Like humans, chimpanzees and gorillas have demonstrated characteristics of symbolic language (Savage-Rumbaugh et al. 1986; Patterson and Linden 1981). Similar asymmetries have not been found in the brains of old-world monkeys, but other interesting facets related to communication have been identified. In a study of rhesus monkeys, metabolic activity was compared between the left and right hemisphere when either control sounds or species-specific monkey calls were played (Poremba et al. 2004). It was revealed that significantly greater metabolic activity occurred in the left superior temporal gyrus but only in response to the monkey calls rather than the control sounds. Rhesus monkeys do not have a similar structure to Broca's area, but these results indicate that there was perhaps a hemispheric specialization for interpreting sounds used in communication that could have preceded the vocal complexities associated with language.

Electrophysiological asymmetries in the hand representation of primary motor cortex (area 4) were correlated with hand preference in squirrel monkeys and involved larger surface area for

hand movement and greater spatial complexity of the motor movement representations in the dominant hemisphere (Nudo et al. 1992). Squirrel monkeys do not have a population-level hand preference but the neural control asymmetries were consistent with the preferred hand of each animal tested.

Potential factors that could have preceded motor lateralization may be seen in non-primate species and generally involve lateralized differences in perceptual abilities or social behavior (for review see Rogers and Andrew 2002; Vallortigara 2006). Many studies in rodent, bird, reptile, and amphibian species have found population-level tendencies for pawedness, prey capture, social behaviors related to courtship, and aggression. After more than 150 years of study, much has been written about cerebral lateralized structures and functions, but few phyletic comparisons reveal a simple evolutionary progression from sensory to motoric lateralization. What is apparent is that lateralized functions and associated cerebral asymmetries do exist and must confer an advantage to the animal in order to be selected for. It may be the case that these selection pressures function differently not only between species but also within individuals of the same species. How the human species became so rigidly lateralized for speech functions remains a valid question for research, but it is also important to understand the factors that influence lateralization in other species as well.

## Cross-References

- ▶ [Behavioral Lateralization](#)
- ▶ [Cerebral asymmetry](#)
- ▶ [Dextral](#)
- ▶ [Feeding Behavior](#)
- ▶ [Hand Preference](#)
- ▶ [Hemispheric Specialization](#)
- ▶ [Language](#)
- ▶ [Manual Specialization](#)
- ▶ [Posture](#)
- ▶ [Sinistral](#)

## References

- Broca, M. P. (1861). Remarques sur le siege de la faculte du langage articule, suivies d'une observation d'aphemie (perte de la parole). *Bulletin de la Société Anatomique*, 6, 330–357.
- Cantalupo, C., & Hopkins, W. D. (2001). Asymmetric Broca's area in great apes. *Nature*, 414, 505.
- Corballis, M. C. (1991). *The lopsided ape*. New York: Oxford.
- Hecaen, H., & Ajuriaguerra, J. (1964). *Left handedness*. New York: Grune & Stratton.
- Hopkins, W. D. (1999). On the other hand: Statistical issues in the assessment and interpretation of hand preference data in nonhuman primates. *International Journal of Primatology*, 20(6), 851–866.
- Hopkins, W. D. (2007). In W. D. Hopkins (Ed.), *The evolution of hemispheric specialization in primates*. Burlington, MA: Academic Press/Elsevier.
- Kimura, D. (1976). The neural theory of language qua gesture. In H. Whitaker & H. A. Whitaker (Eds.), *Studies in neurolinguistics* (Vol. 2). New York: Academic.
- MacNeilage, P. F. (2007). Present status of the postural origins theory. In W. D. Hopkins (Ed.), *The evolution of hemispheric specialization in primates* (pp. 59–91). Burlington, MA: Academic Press/Elsevier.
- MacNeilage, P. F., Studdert-Kennedy, M. G., & Lindblom, B. (1987). Primate handedness reconsidered. *Behavioral & Brain Sciences*, 10, 247–303.
- McGrew, W. C., & Marchant, L. F. (1997). On the other hand: Current issues in and meta-analysis of the behavioral laterality of hand function in nonhuman primates. *Yearbook of Physical Anthropology*, 40, 201–232.
- Meguerditchian, A., Vauclair, J., & Hopkins, W. D. (2013). On the origins of human handedness and language: A comparative review of hand preferences for bimanual coordinated actions and gestural communication in nonhuman primates. *Developmental Psychobiology*, 55, 637.
- Napier, J. (1980). *Hands*. London: George Allen & Unwin.
- Nudo, R. J., & Masterton, R. B. (1990). Descending pathways to the spinal cord, IV: Some factors related to the amount of cortex devoted to the corticospinal tract. *Journal of Comparative Neurology*, 296, 584–597.
- Nudo, R. J., Jenkins, W. M., Merzenich, M. M., Prejean, T., & Grenda, R. (1992). Neurophysiological correlates of hand preference in primary motor cortex of adult squirrel monkeys. *Journal of Neuroscience*, 12, 2918–2947.
- Nudo, R. J., Sutherland, D. P., & Masterton, R. B. (1995). Variation and evolution of mammalian corticospinal somata with special reference to primates. *Journal of Comparative Neurology*, 358(2), 181–205.
- Patterson, F. G., & Linden, E. (1981). *The education of Koko*. New York: Holt, Rinehart and Winston.
- Poremba, A., Malloy, M., Saunders, R. C., Carson, R. E., Herscovitch, P., & Mishkin, M. (2004). Species-specific calls evoke asymmetric activity in the monkey's temporal poles. *Nature*, 427, 448.
- Preuschoft, H., & Chivers, D. J. (Eds.). (1993). *Hands of primates*. New York: Springer.
- Rogers, L. J., & Andrew, R. J. (2002). *Comparative vertebrate lateralization*. Cambridge: Cambridge University Press.
- Savage-Rumbaugh, E. S., McDonald, K., Sevcik, R. A., Hopkins, W. D., & Rupert, E. (1986). Spontaneous symbol acquisition and communicative use by pygmy chimpanzees (*Pan paniscus*). *Journal of Experimental Psychology: General*, 115, 211–235.
- Seltzer, C. P., Forsythe, C., & Ward, J. P. (1990). Multiple measures of motor lateralization in human primates (*Homo sapiens*). *Journal of Comparative Psychology*, 104(2), 159–166.
- Vallortigara, G. (2006). The evolution of behavioral and brain asymmetries: Bridging together neurophysiology and evolutionary biology. In Y. Malashichev & W. Dechel (Eds.), *Behavioral and morphological asymmetries in vertebrates*. Austin: Landes Bioscience.
- Ward, J. P., Milliken, G. W., & Stafford, D. K. (1993). Patterns of lateralized behavior in prosimians. In J. P. Ward & W. D. Hopkins (Eds.), *Primate laterality: Current behavioral evidence of primate asymmetries*. New York: Springer.
- Watson, S. L., & Hanbury, D. B. (2007). Prosimian primates as models of laterality. In W. D. Hopkins (Ed.), *The evolution of hemispheric specialization in primates* (pp. 228–250). Burlington, MA: Academic Press/Elsevier.

# P

## Prosimian Locomotion

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### Definition

Anthropoid	Primate group including Old World monkeys, New World monkeys, and apes. Largely diurnal, arboreal (but many species are terrestrial), and larger-bodied.
Cantilever	A method of locomotion where the hind limbs are fixed to a tree branch to support the upper body in reaching activities.
Locomotion	The movements and postures used by any animal.
Prosimian	Primate group including lorises, galagos, lemurs, sifakas, and tarsiers. Largely nocturnal, arboreal, and small-bodied.

**Quadrupedalism** A form of locomotion where all four limbs are used to move horizontally across a substrate.

### Introduction

Locomotion encompasses the movements and postures that vertebrates use in day-to-day activities, especially in obtaining food, avoiding predators, and finding mates. Primates are specialists at arboreal locomotion and specifically at navigating life in the trees among small branches (Sussman 1999; Ankel-Simons 2007; Fleagle 2013). Among mammals, primates are remarkable in having an unusually high range of locomotor behaviors. They leap, walk quadrupedally, suspend from branches using their tail or feet, brachiate, climb, cling, and cantilever (Fleagle 2013). Despite this large range of locomotor behaviors, primates have relatively few postcranial morphological specializations that reflect these locomotor niches.

Grasping hands and feet with a divergent first digit (the first digit being called the “pollex” in the hand and the “hallux” in the foot) are one of the defining morphological adaptations in primates linked to the arboreal lifestyle (Cachel 2015). Unlike other mammals primates have nails instead of claws which support the soft tissue tactile ridges (dermatoglyphics) present on the digits. All primates (humans included) possess these dermatoglyphic patterns on the palms of their hands

and soles of their feet (including at the end of the digits, i.e., fingerprints). The papillary ridges of the hands and feet provide a source of friction during locomotion and object manipulation. Some primates also possess dermatoglyphic patterns on the skin of other organs. The distal third of the ventral surface of the prehensile tail of ateline monkeys is marked by a friction pad replete with papillary ridges (Organ 2017; Organ et al. 2011), which functions to provide sufficient friction during tail-assisted locomotion. The tarsier *Tarsius bancanus* also possesses a friction pad on the tail, although in this case it is located on the ventroproximal aspect of the tail and is used to prop the body during vertical clinging and resting activities (Sprankel 1965).

Lastly, primates are unique among mammals in the structure of the eyes and the bony components of the skull that holds the eyes. Non-primate arboreal mammals, such as squirrels, have eyes located on the sides of the head. Primates have both eyes situated at the front of the skull in an arrangement called “orbital convergence” (Ankel-Simons 2007; Fleagle 2013). This allows for overlapping visual fields and binocular (stereoscopic) vision. Living a successful arboreal lifestyle high in the forest canopy with thick vegetation is tied to accurate three-dimensional vision, which is necessary for locomotor planning (think about leaping from branch to branch high off the ground) as well as catching insects. Binocular vision allows for this three-dimensional vision.

Primates can be broadly organized into two groups (Fig. 1). The prosimians (“pre-monkeys”) consist of lorisiforms, lemuriforms, and tarsiers. They are considered to be the more “primitive” group of primates and more representative of what the earliest primates may have looked like. They also are considered good models of how the earliest primates may have behaved because the fossil record indicates that the earliest primates were morphologically similar to tarsiers or galagos, thus likely arboreal (Sussman 1999; Covert 2002; Cachel 2015). Anthropoids (Old World monkeys, New World monkeys, and apes) are considered to be more “derived” than prosimians.

This entry provides first a summary of the prosimians, who they are, what they look like, how

they live, and how they behave, and then moves into the factors that influence development of particular locomotor styles. Lastly, this entry provides a summary of the types of locomotion within the prosimians with illustrations of each type.

## Prosimian Lifestyles

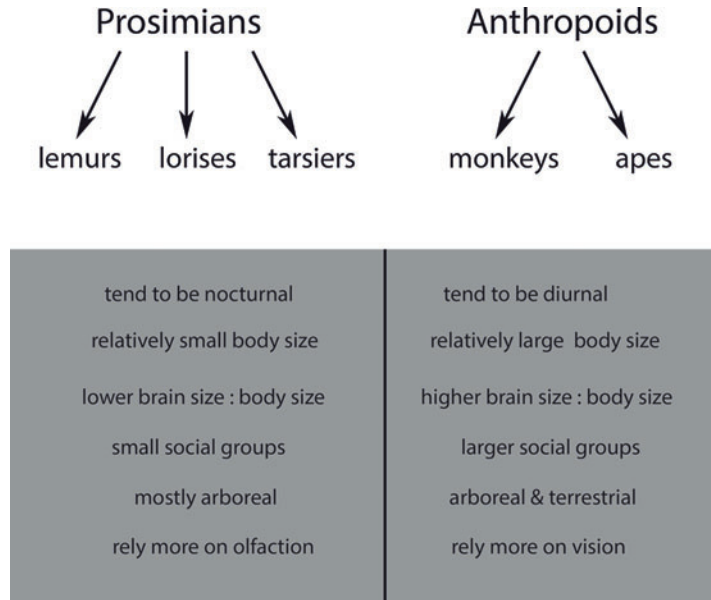
Prosimians include the lorisiforms, lemuriforms, and tarsiers (see Fig. 2). Lorisiforms include the Asian lorises (slow lorises and slender lorises), African lorises (pottos and angwantibos), and galagos (bush babies). Slow lorises (*Nycticebus* spp.) and slender lorises (*Loris* spp.) are widely distributed in southern India, Sri Lanka, and throughout much of Southeast Asia (Nekaris and Bearder 2007). Pottos (*Perodicticus* spp.) and angwantibos (*Arctocebus* spp.) are found through much of central Africa (Nekaris and Bearder 2007). Galagos (*Euoticus* spp., *Galago* spp., *Galagoidea* spp., *Otolemur* spp., and *Sciurocheirus* spp.) are scattered throughout eastern, southern, and central Africa (Nekaris and Bearder 2007).

Lemuriforms are found only on the island of Madagascar and include the aye-aye (*Daubentonia* spp.), indriids (*Avahi* spp., *Indri* spp., and *Propithecus* spp.), bamboo lemurs and lemurs (*Eulemur* spp., *Haplemur* spp., *Lemur catta*, *Phaner furcifer*, *Varecia* spp.), mouse lemurs and dwarf lemurs (*Allocebus* spp., *Cheirogaleus* spp., *Microcebus* spp., and *Mirza* spp.), and sportive lemurs (*Lepilemur* spp.) (Gould and Sauther 2007). The tarsiers (*Carlito* spp., *Cephalopachus* spp., and *Tarsius* spp.) are found in the Philippines and the islands of Southeast Asia (Shekelle et al. 2010). While their phylogenetic affinities are debated (Hartig et al. 2013; Kumar et al. 2013), they are grouped here with the lorisiforms and lemuriforms on the basis of their behavior, ecology, and some morphological features.

While there is great diversity within the prosimians, they can be described as sharing several fundamental behavioral and morphological characteristics to the exclusion of anthropoids (Fig. 1).

**Prosimian Locomotion,**

**Fig. 1** The classification of the order Primate into prosimians and anthropoids, with major defining characteristics of each group



Prosimians are almost exclusively nocturnal and arboreal (Sussman 1999); ring-tailed lemurs (Fig. 3) and sifakas (Fig. 4) are the only prosimians that spend any regular time on the ground (ring-tailed lemurs spend up to 30% of waking time on the ground but sifakas come to the ground with less frequency), and, as shown in Fig. 2, they are two of the very few diurnal prosimians (Fleagle 2013).

Life in an arboreal environment does not typically support large social groups (see Liebal et al. 2013). Correspondingly, most prosimian species live in groups where sizes range from 2 to 3 individuals up to 12 individuals. The terrestrial ring-tailed lemurs (*L. catta*) are noted for consistently having large groups, sometimes in excess of 25 individuals, with a relatively complex social hierarchy system and a heavy reliance on stink bomb warfare (Gould and Sauther 2007; Liebal et al. 2013).

Prosimians have a smaller brain size: body size ratio than anthropoids, which may be related to their heavier dependence on olfaction and less dependence on vision in social communication. They also tend to have a smaller body size relative to anthropoids, which is likely related to development of locomotor styles (Ankel-Simons 2007; Liebal et al. 2013).

**Body Size and Locomotion**

Locomotor behavior is influenced by numerous factors such as diet, social behavior, and skeletal morphology. However, body size is perhaps the most influential factor in locomotor style (Merritt 2010). Small mammals tend to be prey more often than predator. This in turn may push some small mammals to be nocturnal rather than diurnal, a mechanism for “hiding” from some predators. Being an arboreal mammal can also be a means of hiding from predators, with some notable exceptions such as snakes (Merritt 2010).

Small mammals, weighing less, can often inhabit arboreal environments that would only support a relatively low body weight, such as thin, narrow branches (the so-called fine branch arboreal niche). Combined with increased avoidance of predators, a small body size is typically associated with arboreality in primates, many of whom are found within Prosimii (Fleagle 2013). Only the larger prosimians, such as the ring-tailed lemurs (Figs. 2 and 3) and sifakas (Figs. 2 and 4), routinely spend time on the ground out of the trees. While still subject to some predation, these larger prosimians are not subject to predation pressure as intensely as the smaller prosimians (Sussman 1999).

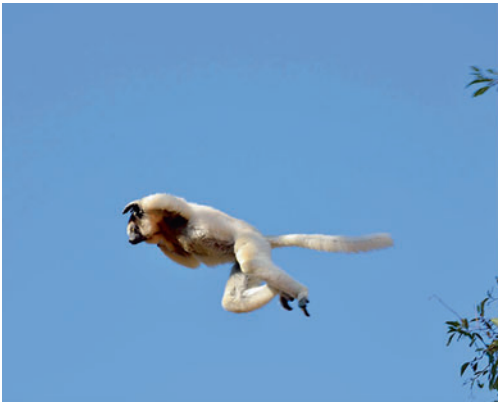


	Lorisiformes			Lemuriformes						Tarsiiformes
	Loridae	Galagonidae	Lemuridae	Cheirogaleidae	Lepilimuridae	Indridae	Daubentonidae	Tarsiidae		
Infraorder										
Family										
Species (common name)	slow lorises ( <i>Nycticebus</i> ) slender lorises ( <i>Loris</i> ) potitos ( <i>Perodicticus</i> ) angwanitobos ( <i>Arctocebus</i> )	galagos ( <i>Galago</i> , <i>Galagoides</i> , <i>Euroticus</i> , <i>Sciuorchirus</i> , & <i>Otolemur</i> )	ring-tailed ( <i>Lemur catta</i> ) ruffed ( <i>Varecia</i> ) eulemurs ( <i>Eulemur</i> ) bamboo lemurs ( <i>Hapalemur</i> )	mouse lemurs ( <i>Microcebus</i> ) dwarf lemurs ( <i>Allocebus</i> , <i>Cheirogaleus</i> , & <i>Mirza</i> )	sportive lemurs ( <i>Lepilemur</i> )	sifakas ( <i>Propithecus</i> ) indrids ( <i>Indri</i> ) avahis ( <i>Avahi</i> )	aye-ayes ( <i>Daubentonia</i> )	tarsiers		
Body Size (mouse = 20g, house cat = 4,500g)	370g-1400g ( <i>Nycticebus</i> ) 103g-322g ( <i>Loris</i> ) 847g-1858g ( <i>Perodicticus</i> ) 150g-325g ( <i>Arctocebus</i> )	162g-360g ( <i>Galago</i> ) 45g-183g ( <i>Galagoides</i> ) 182g-360g ( <i>Euroticus</i> ) 258g-502g ( <i>Sciuorchirus</i> ) 604g-1258g ( <i>Otolemur</i> )	~2.2kg ( <i>L. catta</i> ) 3kg-4kg ( <i>Varecia</i> ) 1.5kg-2.5kg ( <i>Eulemur</i> ) 700g-2400g ( <i>Hapalemur</i> )	30g-90g ( <i>Microcebus</i> ) 75-80g ( <i>Allocebus</i> ) 75-200g ( <i>Cheirogaleus</i> ) 300g ( <i>Mirza</i> )	700g - 900g	2.8kg-6.9kg ( <i>Propithecus</i> ) 6.5kg-6.9kg ( <i>Indri</i> ) 600g-1200g ( <i>Avahi</i> )	2,000g	100g-150g		
Locomotion	"slow climbers" AQ, C ( <i>Nycticebus</i> & <i>Loris</i> ) AQ ( <i>Perodicticus</i> & <i>Arctocebus</i> )	VCL or "hoppers" ( <i>Galago</i> , <i>Galagoides</i> , <i>Euroticus</i> , <i>Sciuorchirus</i> ) AQ ( <i>Otolemur</i> )	AQ ( <i>Varecia</i> & <i>Eulemur</i> ) AQ & TO ( <i>L. catta</i> ) VCL & AQ ( <i>Hapalemur</i> )	AQ	VCL	VCL, TBH, AQ, TQ ( <i>Propithecus</i> ) VCL, AQ, TQ ( <i>Indri</i> ) VCL, AQ ( <i>Avahi</i> )	AQ	VCL		
Predation Pressure	for <i>Loris</i> , relatively high; unclear for others	relatively high for most	relatively low	high	high	relatively low	relatively low (except for humans)	high		
Diet	<i>Nycticebus</i> : gums & fruit; <i>Loris</i> : animal prey; <i>Perodicticus</i> & <i>Arctocebus</i> : animal prey & fruit	<i>Galago</i> & <i>Euroticus</i> : gums & animal prey; <i>Galagoides</i> & <i>Sciuorchirus</i> : fruit & animal prey; <i>Otolemur</i> : gums, fruit, & animal prey	<i>L. catta</i> & <i>Eulemur</i> : leaves, fruit, bark, sap, & flowers; <i>Varecia</i> : fruit <i>Hapalemur</i> : bamboo & fruit	<i>Microcebus</i> : gums, fruit, insects <i>Allocebus</i> , <i>Cheirogaleus</i> , & <i>Mirza</i> : nectar & fruit	fruit & leaves	<i>Propithecus</i> & <i>Indri</i> : leaves with some fruit; <i>Avahi</i> : leaves	larvae, insects, seeds, fruit, & nectar	insects, lizards		

**Prosimian Locomotion, Fig. 2** The major groups within the Prosimii, characteristics linked to their lifestyle, and major locomotor categories of each group. *AQ* arboreal quadrupedalism, *C* cantilever, *VCL* vertical clinging and leaping, *TQ* terrestrial quadrupedalism, *TBH* terrestrial bipedal hopping

**Prosimian Locomotion,**

**Fig. 3** Ring-tailed lemurs (*Lemur catta*) in a terrestrial quadrupedal stance. Ring-tailed lemurs are the only prosimian group that routinely spend lengths of time on the ground. Note the divergent first digit on the hand and foot, helpful in maintaining a grasp on small tree branches (Photo credit Hajarimanitra Rambeloarivony)



**Prosimian Locomotion, Fig. 4** *Left Image:* sifaka (*Propithecus* spp.) performing a spectacular aerial leap across the forest canopy. These vertical clinging and leaping prosimians push off of the tree limb with their powerful

hind limbs and fly through the air. *Right Image:* group of sifakas hopping bipedally on the ground with upper limbs extended to the side (Photo credit Hajarimanitra Rambeloarivony)

Lastly, body size has an important influence on dietary requirements in mammals. Smaller mammals have higher metabolisms than larger mammals and tend to need a higher quality diet with greater percentages of protein relative to larger mammals (Merritt 2010). Protein is typically represented in the form of other animals such as insects, young birds/eggs, and small reptiles. These food sources may be rare in any given arboreal environment and typically are not eager to be prey items so they may have to be chased and captured. Within primates this type of food is often associated with fast styles of locomotion such as leaping, hopping, or running. Larger mammals have slower metabolisms than small

mammals and can afford to subsist on relatively low quality but plentiful foods such as leaves, which don't need to be caught. Within primates this type of diet is often associated with slower styles of locomotion such as arboreal quadrupedalism or slow climbing (Ankel-Simons 2007; Fleagle 2013).

### **Ways to Get Around as a Prosimian, or Locomotor Styles**

Locomotion among prosimians takes widely divergent forms (see Fig. 2). With increasing body size, the amount of climbing in prosimians

increases and the amount of leaping decreases (with the vexing and obvious exception of sifakas, who make spectacular leaps at their large body size – Fig. 4). Among primates in general, locomotion can be classified into four major types: vertical clinging and leaping (VCL), quadrupedalism (both arboreal and terrestrial varieties), brachiation, and bipedalism. Many primates adopt a mix of these locomotor styles throughout their activity cycle, depending upon which substrate they are using at any given time and what the goal of their movement is (gathering food, agonistic encounters, predator avoidance, etc.). Within these four major types of locomotion, there are a number of subtypes, such as arboreal versus terrestrial quadrupedalism, and the differences between the categories lie primarily in the degree to which the forelimbs versus hind limbs are used to climb, swing, jump, and run.

Small-bodied prosimians tend to be arborealists and exploit quadrupedalism and/or vertical clinging and leaping. The smallest prosimians tend to be committed vertical clingers/leapers and are the small galagos, weighing in at 50 g–450 g (*Galago*, *Galagoides*, *Sciurocheirus*), and the tarsiers, weighing in at 60 g–150 g (*Carlito*, *Cephalopachus*, and *Tarsius*), as shown in Fig. 5. The tiniest lemuriforms of Madagascar are the mouse lemurs weighing in around 50 g (see Fig. 2). These diminutive prosimians use both arboreal quadrupedal running and vertical clinging and leaping (Fig. 6), all occurring along the smallest branches of trees. This is a rare locomotion style for large prosimians. Sifakas (*Propithecus* spp.) are enormous among the prosimians, weighing in around 6 kg, well above the average house cat. These diurnal prosimians are vertical clingers and spectacular leapers (see Fig. 4). No doubt due in part to their large body size, sifakas spend time on the ground and employ a unique style of locomotion, bipedal hopping (Fig. 6).

### Vertical Clinging and Leaping (VCL)

This locomotor mode involves, as its name suggests, clinging to a relatively narrow vertical tree branch with both forelimb and hind limbs (e.g.,

see Fig. 5). Vertical clingers and leapers – typically small-bodied prosimians – largely avoid going to the ground by using long-distance, ricochet leaps to get from tree to tree. Using the hind limbs and powerful hamstring muscles, these primates push off of the vertical substrate and reach for the upcoming substrate with their forelimbs. VCL is a fast way of moving that can be helpful in avoiding predators and catching animal prey.

### Arboreal Quadrupedalism

The vast majority of primate species are arboreal (Fleagle 2013) and most prosimians adhere to this general rule (see Fig. 2). The conservation of quadrupedalism in primates is evident in examinations of the primate fossil record as well, with indications that the earliest primates included some quadrupedalism in their locomotor repertoire as well (Larson 1998). Arboreal quadrupedalism is the preferred mode of locomotion for the larger galagos (*Otolemur* spp., Fig. 7), lorises (Fig. 8) and pottos and all lemuriforms except sifakas and sportive lemurs. Among the arboreal quadrupeds, slow lorises and slender lorises (*Nycticebus* and *Loris*) stand out for their remarkably slow method of advancement. While most of the small galagos and the tarsiers are rapid VCLs, lorises take an opposite approach.

Quadrupedalism in primates is somewhat different than in most other quadrupedal mammals. While many mammals move quadrupedally, primates do so using a high degree of forelimb protraction with a diagonal, couplet gait. This diagonal gait allows only one limb to be off the substrate at any one time, increasing contact on curved, narrow branches and proffering added stability in the canopy (Larson and Stern 2006; Schmitt 1998; Schmitt et al. 2006).

Whether done in the trees or on the ground, primate quadrupeds tend to protract their upper limbs to a higher extent than other mammalian quadrupeds (Schmitt 1998; Schmitt et al. 2006). Protracting the forelimbs may produce a longer stride, reducing the frequency of gait. This sort of gait pattern may be useful in reducing the branch sway during quadrupedal walking, thereby reducing the danger of falling off the branch and



**Prosimian Locomotion, Fig. 5** Tarsier (*Tarsius* spp.) clinging onto a tree branch in a typical posture. Tarsiers are categorized as vertical clingers and leapers. Note the characteristic large eyes in this nocturnal prosimian as well as the flattened nails on the hands and feet (Photo credit Sharon Gursky)



**Prosimian Locomotion, Fig. 6** A mouse lemur (*Microcebus* spp.) clinging onto a spiny tree in the spiny forest of Madagascar. These lemuriforms are among the smallest of the prosimians and use both vertical clinging and leaping and arboreal quadrupedalism (Photo credit Hajarimanitra Rambeloarivony)

alerting potential prey. Primate quadrupeds also use a diagonal gait or diagonal couplet where opposite forelimbs and hind limbs move together.

Lorises are among the most carnivorous of all primate species (feeding on insects and small reptiles). Instead of rapidly approaching their prey like carnivorous galagos and tarsiers, lorises tend to take a slow, stealthy approach. Lorises, especially slow lorises, are also remarkable in their use of cantilevering in moving through small branches. Cantilevering is a mechanism by which the hind limbs are fixed in grasping a small branch, while the rest of the body projects forward, not unlike a cantilevered beam (see Fig. 8).

### Terrestrial Quadrupedalism

Very few prosimian species come down from the trees to move quadrupedally on the ground, with

the notable exception of *L. catta* (Fig. 3). The very small prosimians, such as tarsiers, mouse lemurs, and some galagos, prefer to stay in the trees which may provide some protection against predation. The larger *L. catta* spends almost a third of its waking time on the ground in a variety of activities. While there are no definitive explanations for why ring-tailed lemurs spend so much time on the ground, it may be associated with their highly complex social behavior and relatively large social groups. Ring-tailed lemurs are indeed preyed upon by fossae, raptors, boas, and civets but predation pressure varies from site to site. Functionally, terrestrial quadrupedalism is similar to arboreal quadrupedalism with the main difference being differences in substrate compliance.



**Prosimian Locomotion,**

**Fig. 7** One of the larger galago species, *Otolemur crassicaudatus*, using arboreal quadrupedalism on a small branch. Note the grasping hands and feet in this galago as it moves along the branch (Photo credit Simon Bearder, Nocturnal Primate Research Group, Oxford Brookes University)

**Prosimian Locomotion,**

**Fig. 8** *Upper image:* slow loris (*Nycticebus coucang*) in preparation for a cantilever stance. Note the widely divergent lower limbs grasping onto small branches to support the rest of the body as the cantilever begins. *Lower image:* same slow loris from below in a full cantilever body. Note the fixed hind limbs and the forelimbs reaching ahead (Photo credit Andrew Walmsley, Little Fireface Project)

**Bipedalism**

The only prosimian that engages in any sort of routine bipedal locomotion is the sifaka (*Propithecus* spp.). Figure 4 shows a typical bipedal hopping bout in an adult sifaka. While these large-bodied primates are usually a VCL

when in an arboreal setting, they come to the ground with varying frequency. Instead of using quadrupedal locomotion when terrestrial, they engage in a hopping behavior with their hind limbs. Tails are typically extended along with the upper limbs at their sides.

## Conclusion

The focus of this entry was to provide a summary of prosimian diversity, including basic taxonomy, preferred habitats, and unique modes of locomotion employed to navigate those habitats. In brief, prosimians employ a wide range of locomotor repertoires including vertical clinging and leaping, arboreal and terrestrial quadrupedalism, and bipedalism. The preferences for locomotor style are directly tied to issues of body size, with smaller species occupying more arboreal habitats and employing more leaping and quadrupedal walking/running, whereas larger species occupy more terrestrial habitats and use combinations of quadrupedal and bipedal locomotion to negotiate their environments.

## Cross-References

- ▶ [Prosimian Cognition](#)
- ▶ [Prosimian Diet](#)
- ▶ [Prosimian Life History](#)
- ▶ [Prosimian Morphology](#)
- ▶ [Prosimian Navigation](#)

## References

- Ankel-Simons, F. (2007). *Primate anatomy* (3rd ed.). Burlington: Academic Press.
- Cachel, S. (2015). *Fossil primates*. Cambridge: Cambridge University Press.
- Covert, H. H. (2002). The earliest fossil primates and the evolution of prosimians: Introduction. In W. C. Hartwig (Ed.), *The primate fossil record* (pp. 13–20). Cambridge: Cambridge University Press.
- Fleagle, J. G. (2013). *Primate adaptation and evolution* (3rd ed.). San Diego: Academic Press.
- Gould, L., & Sauther, M. (2007). Lemuriformes. In C. J. Campbell, A. Fuentes, K. C. MacKinnon, M. Panger, & S. K. Bearder (Eds.), *Primates in perspective* (pp. 46–72). New York: Oxford University Press.
- Hartig, G., Churakov, G., Warren, W. C., Brosius, J., Makalowski, W., & Schmitz, J. (2013). Retrophylogenomics place tarsiers on the evolutionary branch of anthropoids. *Scientific Reports*. doi:10.1038/srep01756.
- Kumar, V., Hallström, B. M., & Janke, A. (2013). Coalescent-based genome analyses resolve the early branches of the euarhontoglires. *PLoS One*. doi:10.1371/journal.pone.0060019.
- Larson, S. G. (1998). Unique aspects of quadrupedal locomotion in nonhuman primates. In E. Strasser, J. Fleagle, A. Rosenberger, & H. McHenry (Eds.), *Primate locomotion: Recent advances* (pp. 157–174). New York: Springer.
- Larson, S. G., & Stern Jr., J. T. (2006). Maintenance of above-branch balance during primate arboreal quadrupedalism: Coordinated use of forearm rotators and tail motion. *American Journal of Physical Anthropology*, 129, 71–81.
- Liebal, K., Waller, B. M., Burrows, A. M., & Slocombe, K. E. (2013). *Primate communication: A multimodal approach*. Cambridge: Cambridge University Press.
- Merritt, J. F. (2010). *The biology of small mammals*. Baltimore: The Johns Hopkins University Press.
- Nekaris, A., & Bearder, S. K. (2007). The loriform primates of Asia and mainland Africa. In C. J. Campbell, A. Fuentes, K. C. MacKinnon, M. Panger, & S. K. Bearder (Eds.), *Primates in perspective* (pp. 24–45). New York: Oxford University Press.
- Organ, J. M., Muchlinski, M. N., & Deane, A. S. (2011). Mechanoreceptivity of prehensile tail skin varies between ateline and cebine primates. *The Anatomical Record*, 294, 2064–2072.
- Organ, J. M. (2017). Dermatoglyphics. In: A. Fuentes (Ed.), *The International Encyclopedia of Primatology* (pp. 1–3). New York: Wiley-Blackwell.
- Schmitt, D. (1998). Forelimb mechanics during arboreal and terrestrial quadrupedalism in Old World monkeys. In E. Strasser, J. Fleagle, A. Rosenberger, & H. McHenry (Eds.), *Primate locomotion: Recent advances* (pp. 175–201). New York: Springer.
- Schmitt, D., Cartmill, M., Griffin, T. M., Hanna, J. B., & Lemelin, P. (2006). Adaptive value of ambling gaits in primates and other mammals. *Journal of Experimental Biology*, 209, 2042–2049.
- Shekelle, M., Meier, R., Wahyu, I., Wirdateti, T., & N. (2010). Molecular phylogenetics and chronometrics of Tarsiidae based on 12S mtDNA haplotypes: Evidence for Miocene origins of crown tarsiers and numerous species within the Sulawesi clade. *International Journal of Primatology*, 31, 1083–1106.
- Sprankel, H. (1965). Untersuchungen an *Tarsius*. *Folia Primatologica*, 3(2–3), 153–188.
- Sussman, R. W. (1999). *Primate ecology and social structure. volume 1: Lorises, lemurs and tarsiers*. Needham Heights: Pearson Custom Publishing.



# P

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## Prosimian Navigation

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### Definition

Navigation – the intentional act of determining and maintaining a route from one place to another (Gallistel 1990).

### Introduction

Prosimians are comprised of three infraorders: Tarsiiformes, Lorisiformes, and Lemuriformes. Few studies focus on prosimian navigation to the same extent as it is studied in other animals; instead aspects of navigation are incorporated into analyses of foraging and dispersal patterns. Call and Tomosello (1997) noted the limited amount of information on spatial cognition in prosimians, emphasizing that further research was needed to discover their capacity for negotiating their environment. Knowledge on this topic is continuously expanding and with an increase in dedicated research, new findings will shed light on the navigational capacity of these primates. Here I summarize findings on navigational

behavior in prosimians including directed searches, such as, foraging patterns.

### Tarsiiformes

Researchers working on habitat utilization and behaviors clearly show that *Tarsus* species travel to goal locations and engage in exploratory movement and nonrandom use of their homeranges. Path lengths in *Tarsius diana* of Kamarora fluctuated based on habitat disturbance compared to those in more pristine forests (Merker 2006), suggesting that these individuals are in search of specific resources lacking in the disturbed areas. *Tarsius syrichta* males frequently move along the periphery of their homerange and traveled from one end to the other, presumably to survey their territory. Females regularly followed the same path for several nights and then changed to a new travel path (Neri-Arboleda et al. 2002). Minimum nightly travel varies between species, where *T. syrichta* (260–556 m) travel less than *Tarsius bancanus* (Crompton and Andau 1987) and *Tarsius spectrum* (Gursky 1997; Dagosto et al. 2001). No studies on more complex navigational skills, including mental map use, are reported for tarsiers.

### Lorisiformes

Traveling and foraging make up as much as 50% of nightly activity in *Loris* species, where traveling is defined as directed movement (Nekaris 2001). Lorises traveled along the perimeter of their home ranges, for territorial purposes, similar to tarsiers

species. Males were also observed traveling in a direct line for more than 50 meters to reach female conspecifics (Nekaris 2001, 2003). *Nycticebus* species also display goal-oriented travel. The Javan slow loris likely uses route-based mental maps to navigate their environment. Other species of slow lorises possess many of the same feeding and behavioral characteristics as the Javan slow loris, thus likely use some form of mental representation, as well, to return to immobile resources, including parked infants (Fitch-Snyder and Ehrlich 2003). *Galago* species utilize gum, another immobile food resource, which requires nonrandom use of their homerange and directed travel to regularly find gum-producing tree and return to its location.

### Lemuriformes

Following a number of studies including Lemuriformes, all consistently report that they do not randomly move within their environment, a preliminary indicator of higher navigational skills. *Propithecus edwardsi*, *Eulemur fulvus rufus*, *Microcebus murinus*, *Eulemur rubriventer*, *Eulemur rufifrons*, and *Varecia variegata editorum* all display nonrandom use of their environment, leading researchers to acknowledge that they utilized distinct routes when traveling from point A to point B (Everhart and Overdorff 2008; Lühns et al. 2009; Razafindratsima et al. 2014; Joly and Zimmerman 2011; Schliehe-Diecks et al. 2012). *P. edwardsi* and *E. f. rufus* uses “traditional” travel routes to get from one food patch to the next. Through the use of “traditional” travel routes, animals are able to check the status of various resources along the way as they move from one important food source to another (Milton 2000), particularly resources that are out of sight from their current location. Similar to *P. edwardsi* and *E. f. rufus*, *M. murinus*, *E. rubriventer*, *E. rufifrons*, and *V. v. editorum* all reused particular routes to travel between feeding resources (Lühns et al. 2009; Razafindratsima et al. 2014), where *E. rufifrons* displayed frequent backtracking behavior. Reusing the same routes and feeding locations suggests that these animals have some form of mental representation of their environment. How complex these representations are is a point of debate among those studying spatial cognition and can be

difficult to determine outside of controlled experiments. *M. murinus* uses cues to successfully travel along routes and route overlap than compared to that of larger more social diurnal primates (Joly and Zimmerman 2011). While dispersing, this species moved in a straight line and covered many areas than during normal ranging patterns. Schliehe-Diecks et al. (2012) concluded that these unusual patterns were the result of a standardized exploration/dispersal strategy. Lemuriformes have been the focus of both basic and complex navigational research, providing a much more complete picture of how these species negotiates their environment.

### Conclusion

Navigation, or the act of using an intentional route to move from one location to the next, is seen across a number of animal species. In prosimians, basic navigational skills including foraging patterns and seeking conspecific are seen in all three infraorders. Research focused on more complex navigation like mental mapping is limited to *Nycticebus* species and some Lemuriformes. Though spatial cognition is not a new topic and there is no limit to the amount of research focused on navigation in other animals, there is an emerging interest in expanding this research to include prosimians.

### Cross-References

- ▶ [Computerized Maze Studies in Primates](#)
- ▶ [Nocturnality](#)
- ▶ [Non-Human Primates](#)

### References

- Bearder, S. K., & Martin, R. D. (1980). Acacia gum and its use by bushbabies, *Galago senegalensis* (Primates: Lorisidae). *International Journal of Primatology*, 1 (2), 103–128.
- Crompton, R. H., & Andau, P. M. (1987). Ranging, activity rhythms, and sociality in free-ranging *Tarsius bancanus*: A preliminary report. *International Journal of Primatology*, 8(1), 43–71.

- Dagosto, M., Gebo, D. L., & Dolino, C. (2001). Positional behavior and social organization of the Philippine tarsier (*Tarsius syrichta*). *Primates*, 42(3), 233–243.
- Erhart, E. M., & Overdorff, D. J. (2008). Spatial memory during foraging in prosimian primates: *Propithecus edwardsi* and *Eulemur fulvus rufus*. *Folia Primatologica*, 79(4), 185–196.
- Fitch-Snyder, H., & Ehrlich, A. (2003). Mother-infant interactions in slow lorises (*Nycticebus bengalensis*) and pygmy lorises (*Nycticebus pygmaeus*). *Folia Primatologica*, 74(5–6), 259–271.
- Gallistel, C.R. (1990). *The organization of learning*. Cambridge; The MIT Press.
- Gursky, S. (1997). *Modeling maternal time budgets: The impact of lactation and gestation on the behavior of the spectral tarsier, Tarsius spectrum* (Unpublished PhD thesis). SUNY-Stony Brook.
- Joly, M., & Zimmermann, E. (2011). Do solitary foraging nocturnal mammals plan their routes? *Biology Letters*, 7(4), 638–640.
- Lühns, M. L., Dammhahn, M., Kappeler, P. M., & Fichtel, C. (2009). Spatial memory in the grey mouse lemur (*Microcebus murinus*). *Animal Cognition*, 12(4), 599–609.
- Merker, S. (2006). Habitat-specific ranging patterns of Dians tarsiers (*Tarsius diana*) as revealed by radio-tracking. *American Journal of Primatology*, 68(2), 111–125.
- Milton, K. (2000). Quo vadis? Tactics of food search and group movements in primates and other animals. In S. Boinski & P. A. Garber (Eds.), *On the move: How and why animals travel in groups* (pp. 375–417). Chicago: University of Chicago Press.
- Nekaris, K. A. I. (2001). Activity budget and positional behavior of the Mysore slender loris (*Loris tardigradus lydekkerianus*): Implications for slow climbing locomotion. *Folia Primatologica*, 72(4), 228–241.
- Nekaris, K. A. I. (2003). Observations of mating, birthing and parental behaviour in three subspecies of slender loris (*Loris tardigradus* and *Loris lydekkerianus*) in India and Sri Lanka. *Folia Primatologica*, 74(5–6), 312–336.
- Neri-Arboleda, I., Stott, P., & Arboleda, N. P. (2002). Home ranges, spatial movements and habitat associations of the Philippine tarsier (*Tarsius syrichta*) in Corella, Bohol. *Journal of Zoology*, 257(3), 387–402.
- Razafindratsima, O. H., Jones, T. A., & Dunham, A. E. (2014). Patterns of movement and seed dispersal by three lemur species. *American Journal of Primatology*, 76(1), 84–96.
- Schliehe-Diecks, S., Eberle, M., & Kappeler, P. M. (2012). Walk the line: Dispersal movements of gray mouse lemurs (*Microcebus murinus*). *Behavioral Ecology and Sociobiology*, 66(8), 1175–1185.
- Tomasello, M. & Call, J. (1997). *Primate cognition*. New York: Oxford University Press.

# C

## Catarrhine Communication

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### Synonyms

Apes; Audition; Facial expression; Gesture; Modality; Multimodal; Old world monkeys; Olfaction; Sensory channel; Signal; Touch; Vocalization; Vision

### Definition

Old world monkeys and apes exhibit a large array of visual, acoustic, tactile, and olfactory signals.

### Introduction

Communication presents the foundation for all social behavior of primates, and the need to navigate their complex social environments has contributed to the evolution of sophisticated communication systems (Semple and Higham 2013). This entry provides an overview of communication patterns identified in catarrhines, a primate clade constituting two superfamilies: Cercopithecoidea (old world monkeys) and Hominoidea (apes). Catarrhines are distinguished from other primates by downward-

facing nostrils, opposable thumbs, and a reduced vomeronasal organ, among numerous other traits. Species of this taxon are generally diurnal, live mostly in social groups, and exhibit extended periods of maternal care; characteristics that are thought to have important implications for the evolution of their communicative systems. Catarrhines communicate with conspecifics to solve problems of survival (e.g., predation and defense of food sources), reproduction (e.g., sexual behavior and mother-offspring coordination), and group living (e.g., alliance formation and conflict resolution) (Liebal et al. 2013).

Given the immense variety regarding definitions of communication in the literature, it should be first clarified what this entry considers as a “signal”. Following the “influence” concept of communication, signals represent traits that exert influence on other individuals through sensory stimulation, and have been under selection specifically for their communicative function (Higham and Hebets 2013). In recent years, the communication of catarrhines tended to be mainly divided into three behavioral modalities – gesture, facial expression, and vocalization – encompassing the sensory channels of vision, touch, and audition (Liebal et al. 2013). The comparative research on ape and monkey communicative behavior has been widely used to trace the evolutionary roots of language, often focusing on underlying cognitive abilities such as intentionality and reference (Arbib et al. 2008). Owing to this comparative bias, most reviews of primate communication

focused on behavioral signals only, with communication defined based on assumptions about potential underlying cognitive mechanisms rather than evolutionary function. Defining communication as involving behavior on the signaler's behalf results in the neglect of other important signal types in definitions, such as genital swellings and the bright facial colors of the mandrill *Mandrillus sphinx*. Moreover, the conceptual focus on signal production and form rather than signal perception and function (Semple and Higham 2013) meant that the visual sensory channel has often been treated as two modalities of "gesture" and "facial expression" (Fröhlich 2017). However, to understand the function of animal signals, it is vital to consider the role of receiver perception and thus the receiver's sensory systems that are stimulated (Higham and Hebets 2013). This entry will follow the suggestion of Semple and Higham (2013) and present communication in terms of sensory modalities through which signals are perceived by the recipient, but also with regard to production and the different forms in which they are produced by the signaler.

Catarrhine primates produce and perceive signals in multiple sensory modalities, including the visual, acoustic, tactile, and olfactory channel, which differ in precision with regard to intended receivers ("locatability"), range, and persistence over time ("fade-out time"). Thus, the usage of different sensory modalities is constrained by features of the physical and social environment. In arboreal and densely vegetated settings, visual signals like facial expressions and gestures are transmitted less effectively and are thought to play a less important role than acoustic signals, especially if opportunities for close-range interactions among conspecifics are limited. While we would not expect a large repertoire of visual signals, these environments may favor the evolution of a complex vocal repertoire (Marler 1965). Since catarrhine primates are commonly diurnal, most close-range communication is visual, whereas long-range communication is predominantly audible. Moreover, the social structure and mating system profoundly influences communicative interactions within a species. Primates vary enormously in the complexity of their vocal,

visual, and olfactory signaling repertoires, and the hypothesis that social complexity is linked to communicative complexity (Freeberg et al. 2012) has gained popularity among primatologists in recent years. While there is some evidence that group size in primates is positively correlated with both facial and vocal repertoire (Liebal et al. 2013), these findings should be viewed with caution given that signals are often highly graded, and researchers seldom agree on how to classify repertoires (Semple and Higham 2013). Nonetheless, sociality is supposed to favor the communication via multiple channels, as the interacting animals are spatially close enough to see, hear, smell, and/or touch each other. Multimodal signals may thus be especially suitable for short-distance communication, which is prevalent in many group-living species of the primate order (Marler 1965). Although this entry introduces communication in the sensory modalities of vision, audition, touch, and olfaction separately, it is important to recognize that primates produce and perceive signals rarely in a unimodal format. As outlined below (section "Multimodal Use of Signals"), the simultaneous and sequential organization of signal elements must be considered to decipher complex signal function.

## Visual Communication

Catarrhines rely heavily on visual information, and the role of vision in primates' neural and sociocognitive specialization has been emphasized by several comparative studies. In particular, primates' elaborated visual system has evolved towards high visual acuity compared to most other mammals (Liebal et al. 2013). Catarrhines have evolved a comparably high level of orbital convergence (i.e., eyes facing in the same direction, namely forward), which resulted in binocular visual fields enabling stereotypic vision. Accordingly, the variety of visual signal types is very large, spanning from sexually selected signals like morphological swellings to behavioral signals such as gestures and facial expressions. The main benefits of the visual channel are fast transmission rates, short fade-out times, and the

rapid locatability of the sender. Visual signals like facial expressions and piloerection tend to be effectively perceived only at close proximity to the signaler, but their precision makes them exceptionally suitable for dyadic, close-distance communication.

### Skin Coloration and Swellings

The evolution of uniform trichromatic vision in catarrhines seems to have led to a variety of red skin signals. An extraordinary example of visual communication is presented by the case of mandrill face coloration: males were shown to use the rank-dependent brightness of another male's red coloration to assess individual differences in fighting ability (Setchell and Jean Wickings 2005). Further research on the perception of the facial blue-red contrast suggested that the multicolored face of mandrills represents a multicomponent signal perceived within the same sensory channel (Renoult et al. 2011).

During specific phases of the ovarian cycle, females of numerous catarrhine species exhibit conspicuous swellings of the perineal skin. These hormone-dependent sexual signals are among the largest and the most colorful signals exhibited by any mammal. The exaggerated size of swellings has caused many evolutionary biologists to speculate that sexual selection has strongly influenced their evolution. With respect to signal function, the best-supported theory is probably Nunn's (1999) "graded-signal hypothesis", stating that sexual swelling size contains information about the intra-individual likelihood of ovulation. In this probabilistic model, swellings are larger when the likelihood of ovulation is greater within a cycle. However, the study of swellings has rarely been expanded beyond the element of swelling size. Since mate choice theory poses that males are likely to use multiple signal components of sexual signals, recent studies have emphasized that other visual elements, such as color, shape, and symmetry might also play a role in mate choice. For instance, size of female sexual swellings in female olive baboons *Papio anubis* may facilitate to assess fertility and parity of the signaler, whereas color was shown to be related to parity only (Higham et al. 2008).

### Facial Expression

Catarrhines have a remarkable facial mobility, and most species employ specific facial expressions through movements of the jaws, lips, ears, eyelids, and other facial features. Facial expressions have been commonly assumed to be expressions of emotional states that are largely innate and involuntarily produced (Tomasello 2008). While frequently studied as emotional displays, research has also considered them as true signals, evolved to allow receivers to predict the behavior of senders and to allow senders to manipulate receivers (Waller and Micheletta 2013). Some expressions, like the bared-teeth display, are shared universally among the primate order. The precise meaning and context of the bared-teeth expression can vary between species, but it has long been argued that these similar expressions, including the human smile, comprise homologous traits (van Hooff 1972). Likewise, relaxed open mouth displays are frequently found in the repertoires of different primate species, usually associated with play, and thought to be homologous with human laughter (van Hooff 1972) and playful open mouth expressions seen in other mammals, such as dogs, bears, and even rats (Waller and Micheletta 2013). Facial expressions have been suggested to serve as "meta-communicative" devices to clarify the meaning of ambiguous, potentially agonistic behavior. For example, great apes frequently produce a "play face" when approaching others for play solicitation, presumably to assure that a hitting gesture or wrestling is perceived as intention to play and not as an aggressive approach (Rijksen 1978).

Some facial expressions are less ubiquitous and are only found in specific species or taxa. The "lip-smack" expression, for example, is a dynamic display that involves the fast-paced rapid closing and opening of the mouth and lips (Ghazanfar et al. 2012). Mainly associated with affiliative behaviors (e.g., social grooming) and suggested to facilitate tolerance, it is observed in many old world monkeys, particularly macaques and baboons (Van Hooff 1967). These species often produce lip-smacks during friendly approaches or face-to-face greetings, as well as during mother-infant interactions. While lip-



smacking is a multimodal signal with both an audible and a visual element, the visual component has been shown to be sufficient in rhesus macaques to elicit reciprocation of this signal. Recent studies have highlighted the role “lip-smacking” facial expressions might play for understanding of language precursors, proposing that rhythmic facial movements required for speech production evolved from facial movement patterns in a primate ancestor (Ghazanfar et al. 2012). This theory is based on evidence that the temporal pattern and developmental trajectory of “lip-smacking” (starting with a variable “babbling” phase) in rhesus macaques resembles the timing and ontogeny of speech.

### Visual Gestures

Gestures have been defined as socially directed, mechanically ineffective movements of the extremities, head or body, as well as body postures that exert influence on another individual without coercion (Call and Tomasello 2007). Unlike research on human gesture, which usually focuses on the visual channel, research on primate gestures involves three sensory channels, since gestures can be perceived visually, tactilely, and/or acoustically. Gestural studies, mainly conducted in captive settings, have firmly established that old world monkeys and great apes frequently use visual gestures in their natural intraspecific communication. Visual manual and bodily signals are used in a wide range of social contexts (Call and Tomasello 2007) and are often accompanied by context-dependent facial expressions and postures: For instance, begging gestures solicit food transfers, beckoning gestures initiate sex and submissive gestures (e.g., presenting hindquarters) signal subordination towards a threatening dominant male. Male hamadryas baboons, *Papio hamadryas*, use various visual gestures to coordinate group movement and negotiate travel direction: the so-called notifying behavior involves an “approach – turn body – present hindquarters – look back” sequence, and group travel is initiated often by a male setting off in his preferred direction with a purposeful gait (Fischer and Zinner 2011).

Primates’ employment of visual gestures has often been used to infer whether a particular signal is used in a goal-directed (“intentional”) way. Communicating more/only via visual gestures only when the audience is visually attending and thus receptive to the signal suggests that the sender has an intention to manipulate the receiver’s behavior (Liebal et al. 2013). Recent studies on the gestural development in wild chimpanzee infants suggested that visual gestures increase at the expense of tactile signals with decreasing mother-infant proximity and increasing interaction rates with nonmaternal conspecifics (Fröhlich et al. 2016b). Numerous lines of comparative research suggested that nonhuman primates have considerably more intentional control, flexibility, and interactional awareness of their productive gestural communication than of their vocalizations or facial expressions (Arbib et al. 2008; Tomasello 2008). With accumulating evidence for flexible and goal-directed use of vocalizations and facial expressions, this view has however been alleviated in recent years.

### Acoustic Communication

Sound plays a crucial role for maintaining group cohesion, allowing for long-distance communication with spatially disparate group members in dark and/or densely vegetated environments where opportunities for visual communication are limited. Compared to visual and tactile communication, acoustic signals are seldom targeted precisely at specific receivers, and broadcasted rather indiscriminately. While vocalizations are the most common form of acoustic communication, communication through sound does not always involve the vocal folds: auditory gestures and unvoiced calls are other acoustic communicative means employed by several catarrhine species.

### Vocalizations

Vocalizations are defined as utterances resulting from vibrations of the vocal folds within the larynx, which can exhibit a large variation in acoustic structure. The production of a vocalization

involves air expulsion from the lungs, resulting in rhythmic opening and closing of the vocal folds that can be perceived as sound waves. Frequency, amplitude, and temporal pattern can differ according to recipient and physical environment. With the benefit of traveling large distances, vocalizations function to defend territories and food resources, and to locate conspecifics. Within a social group, vocalizations are produced in contexts like foraging, travel, copulation, and aggression. Research on contact call function in foraging primate troops has revealed that call rate increases with the distance to the nearest neighbor and habitat density (Bradbury and Vehrencamp 1998). With increasing separation distance, Japanese macaques, *Macaca fuscata*, may increase call duration, amplitude, and frequency modulation to enable the reunion with group mates (Koda 2004). Several catarrhine species rely on vocalizations as consensus-building departure signals to coordinate group travel: in mountain gorillas *Gorilla beringei beringei* and chacma baboons *Papio ursinus* several individuals increase the production of grunts before the initiation of travel (Fischer and Zinner 2011), whereas in chimpanzees (*Pan troglodytes*) only particular individuals produce “travel hoos” that seem to be directed at closely bonded individuals (Gruber and Zuberbühler 2013). Social intragroup calls are often not broadcast indiscriminately, but affected by identity and dominance rank of the receivers. Rhesus macaques, *Macaca mulatta*, were shown to give five acoustically different “screams” when interacting with opponents varying in rank, relatedness etc., which elicited different responses from group mates depending on opponent type and agonistic situation (Gouzoules et al. 1984).

While primates’ intragroup calls generally exhibit a lower amplitude and higher acoustic variation, intergroup calls often travel long distances through the environment. Territorial “loud calls”, as produced by gibbons, are thought to function to announce the location of the caller within the territory and to repel other individual and groups. Predator-specific alarm calls are another class of “loud calls”, which can address the predator and close-by group members (Zuberbühler 2001). It has been argued that

alarm calls of several catarrhine species qualify as “functionally referential”, that is, they are correlated with the occurrence of objects or events in the external world of the signaler, and induce the receiver to respond adaptively in the absence of direct cues from the eliciting stimulus. This context-sensitive semanticity has been demonstrated for several species of old world monkeys, with individuals responding to acoustically distinct calls with particular types of antipredator responses even in the absence of the predator. For instance, vervet monkeys *Chlorocebus pygerythrus*, Diana monkeys *Cercopithecus diana*, and Campbell’s monkeys *Cercopithecus campbelli* all use distinct alarm calls for different predators, eliciting appropriate escape responses in other group members (Zuberbühler 2001).

Vocal turn-taking, defined as coordination of vocal contributions by two individuals, has been evidenced in Campbell’s monkeys (Lemasson et al. 2011), and from the lesser apes, siamangs *Hylobates syndactylus* (Geissmann and Orgeldinger 2000). In siamangs, pair-bonded males and females produce loud and ritualized “duetting” vocalizations for territorial defense, but also to strengthen existing pair bonds or to attract new mates (Geissmann and Orgeldinger 2000). Reports of vocal turn-taking in the great apes are limited to reports of male chimpanzees chorusing with pant-hoots, an acoustically distinct long-distance call. Chorusing in male chimpanzees seems to reliably reflect short-term affiliation, facilitating feeding tolerance and predicting support in agonistic interactions (Fedurek et al. 2013).

### Unvoiced Calls

Sounds produced with the mouth but not involving the vocal tract have been termed unvoiced or voiceless calls and include “kiss squeaks”, “raspberries”, “whistles”, and “lip-smacks” (see section “Facial Expression”). The kiss squeak is produced by a sharp intake of air through pursed lips and has been demonstrated to serve as alarm call in wild Bornean, *Pongo pygmaeus*, and Sumatran orangutans, *Pongo abelii*, in response to encounters with potential predators or conspecifics (Rijksen 1978). In some populations, the

“kiss squeak” is performed by positioning a hand or a hand with leaves in front of or against the lips during production (van Schaik et al. 2003). “Raspberries” are spluttering sounds that are produced by orangutans of some wild populations during nest building (van Schaik et al. 2003) and by captive chimpanzees as attention-getting sounds towards their human caretakers (Liebal et al. 2013). Orangutans have been shown to copy “whistling” sounds from humans, demonstrating the ability to acquire a novel voiceless call belonging to a repertoire of a different species. However, although human-ape experimental setups have the potential to reveal apes’ cognitive abilities, they cannot provide insight into strategies that are employed in their natural communication with conspecifics (Liebal et al. 2013).

### Auditory Gestures

The most popular example of a gesture producing sound is probably the gorillas’ “chest-beat”, which is used as part of their display behavior or to invite others to play. Many of the reported auditory gestures in great apes (e.g., “clip leaf” and “slap object”) have been suggested to serve as “attention-getting” signals that do not convey specific information about the context. The signaler’s message might be rather conveyed in the context-typical facial expressions (e.g., “play-face”) or body postures (Tomasello et al. 1994; however, see Liebal et al. (2013) for different view). Most gestures producing a sound element are actually considered audio-visual gestures, as they normally also have salient visual components. Hence, the visual orientation (“attentional state”) of the recipient must always be assessed to infer which components of a signal were salient for perception (Fröhlich 2017). Adult chimpanzees and bonobos are commonly observed to drum on the trunks of trees, by beating their hands and feet against on the hard surface. Drumming by chimpanzees, often accompanied by “pant-hoot” vocalizations, is performed in multiple contexts including traveling, display, inter-group encounter, and when arriving at large food sources (Crockford and Boesch 2005).

### Tactile Communication

Tactile signals, similar to visual signals, enable rapid and precise communication particularly suitable for dyadic, close-distance communication. Out of the four communicative modalities presented, tactile signaling is arguably the most intimate and risky, since it is the only one that requires the renunciation of individual space and, in many cases, the exposition of vulnerable body parts. Surprisingly, touch is often neglected as a communicative channel in reviews of primate communication. Primates rely on tactile signals to resolve conflicts, mediate courtship, reaffirm affiliative and dominance relationships, and coordinate group movements. Tactile appeasement tactics and signals are of particular importance for maintaining peace in groups, involving post-conflict reconciliation, third-party consolation, allogrooming, and greeting displays (Bradbury and Vehrencamp 1998). Reconciliation acts following conflicts frequently involve close contact, particularly the winner approaching and embracing, kissing, or grooming the loser. Chimpanzees are thought to reconcile particularly often after conflicts, but this behavior is also reported for old world monkeys like macaques and baboons. Consolation behavior after conflicts, usually by a closely bonded individual not involved in the conflict, involves embracing, grooming, and other types of touch such as licking and genitogenital rubbing. Third-party consolation is observed in chimpanzees and bonobos but less frequently in old world monkeys (Bradbury and Vehrencamp 1998). Both reconciliation and consolation serve to decrease the occurrence of anxiety behaviors in the victim through comforting or reassuring. Allogrooming, the grooming of another individual, is a universal behavior and probably the most widespread interaction involving touch in catarrhine primates. While one obvious function of this behavior is the removal of parasites and debris from the body surface of the groomed animal, it also serves to reaffirm affiliative bonds or the relative dominance status between groomer and groomee. As a major tension-reducing strategy in primates, allogrooming

can be exchanged for other “goods” such as mating opportunities, tolerance, or agonistic support in future conflicts. Allogrooming has a crucial communicative function, as the act of grooming carries the message that the recipient is considered a valuable social partner, which can be used to infer the partner’s willingness to support each other in high-risk collaborations. It is most commonly observed between related group members, within female matrilineal groups among old world monkeys and among males in chimpanzees, but also beyond kin relationships. In several catarrhine species, individuals greet the arrival of a known conspecific with physical contact, such as when baboon males touch each other’s genitalia, chimpanzees clasp the partner with one arm in a loose embrace, or bonobos engage in mutual genital rubbing.

Tactile gestures can be distinguished from mere physical actions in that they are not mechanically effective (i.e., they do not function through coercion) and communicate a specific intent. For example, gently touching an individual’s back during a grooming session to indicate a desire for that individual to lie down would be a tactile gesture, as opposed to the direct physical action of forcefully pushing the other to the ground. Tactile gestures are particularly common in affiliative contexts like grooming and reassurance. A recent study on play-soliciting signals in immature chimpanzees found that infants used tactile gestures predominantly in interactions with their mothers, with whom predictable outcomes and high familiarity have been established in many previous interactions (Fröhlich et al.).

## Olfactory Communication

Chemical signals, perceived using olfaction, provide the advantage of persisting over time but lack precision with regard to receivers. Old world monkeys, apes, and humans have traditionally been considered as “microsmatic”, with decreased reliance on olfactory senses in comparison to other sensory modalities such as vision. The olfactory system of catarrhines is thought to be

considerably less complex than in prosimians and new world monkeys, as accessory olfactory bulbs (AOBs) are lacking and the vomeronasal organ is markedly reduced (Barton 2006). The majority of evidence for olfactory communication in primates, such as scent and urine marking, stems from prosimians and callitrichids. These taxa possess numerous scent glands producing secretions containing so-called pheromones, substances secreted by an animal with specific effects on the behavior or physiology of conspecific.

However, the importance of olfactory communication in catarrhines has been increasingly recognized in recent years (Vaglio et al. 2016). Odor and the main olfactory system are thought to be involved in sexual and social behaviors, and specifically the attraction of males to estrous females (Barton 2006). Observational studies suggested that pheromones play a critical role in the sexual context, as olfactory inspection (“sniffing”) by male catarrhine primates is commonly observed. Sternal-gland secretions in mandrills have been shown to signal sex, age, male dominance, and possibly individual identity and group membership, suggesting that scent-marking serves territorial functions but also sociosexual functions of communication in this species (Vaglio et al. 2016). Chimpanzee males show an intensified interest in copulation around the period of female ovulation, which has been related to their ability to detect olfactory signals produced by the female at the time of ovulation. A few studies suggest that vaginal secretions during estrus of female chimpanzees contain pheromones that signal reproductive capacity and physiological status. While chimpanzee females produce a mix of volatile fatty acids in vaginal secretions, only isobutyric acid increases during the ovulation period, which might affect male sexual responsiveness (Matsumoto-Oda et al. 2003). However, as the females of many primate species develop sexual swellings varying in shape, size, and color (see section “Skin Coloration and Swellings”), and thereby multicomponent signal of two sensory modalities, it is important to disentangle how these different signal components contribute to male responses.

## Multimodal Use of Signals

Communications systems of primates are intrinsically multimodal, often involving a simultaneous and sequential production of different signal components in multiple sensory channels. In fact, research on catarrhine communication at both the behavioral and neuronal level has demonstrated a widespread capacity to flexibly combine signals from different modalities (Liebal et al. 2013). A vivid example for a complex communicative scenario was described by Higham and Hebets (2013) for the context of sexual behavior: “[...] male baboons are highly aroused by the visual signal of female sexual swellings (which themselves vary in multiple components such as size, shape, symmetry, and colour), which they then touch (possibly to assess how inflated the swelling is), before sniffing the vagina and its secretions, which they then taste. If the male chooses to mate with the female, she is likely to give a copulation call during coitus, which may indicate further aspects of her status to this and other males”.

Fixed multimodal signals are those whose components are obligatorily coupled due to the mechanics of signal production (e.g., a “scream face” necessarily accompanies a “scream” vocalization in chimpanzees) (Smith 1977). By contrast, free multimodal signal combinations are those whose component signals may be produced separately or combined flexibly with other signals (Tomasello 2008). From the perspective of perception, cross-modal integration of vocal and visual signal elements has been shown in both monkeys and great apes, which were able to recognize the correspondence between species-specific facial and vocal expressions, termed “audio-visual matching” or “face/voice integration” (Partan and Marler 2005). From the production side, several studies in both wild and captive environments indicated that great apes use signal combinations conveying context-specific information that would not be available from a single sensory input (Liebal et al. 2013). For instance, male bonobos have been shown to use the same

vocalization (“contest-hoot”) for play and aggression, but add gestures to distinguish between the two contexts (Genty et al. 2014). This way ambiguous messages sent in one channel can be clarified by adding a more specific component in another channel (Partan and Marler 2005).

## Conclusion

Catarrhine primates, like most other animals, produce and perceive signals of various sensory modalities. The modalities employed are thought to underlie the heavy influence of social and ecological factors. Primates are generally thought of as “visual” mammals, as they exhibit an elaborated visual system with forward-directed large eyes enabling stereoscopic vision. Accordingly, the largest variety of signals is found in this domain, including colorful sexual swellings, facial expressions, and gestures. Sound also plays a major role in catarrhine life, with vocalizations used to defend territories and food resources, negotiate social interactions, and to locate conspecifics. Touch is an often-neglected sense of communication in primates, but signals involving body contact have been shown to play an essential role in affiliation and mother-infant coordination. Although primates are traditionally considered microsmatic, olfactory signals (i.e., pheromones) are used by catarrhines in the recognition of the reproductive status of females. Catarrhines frequently combine signals from different sensory modalities simultaneously and sequentially, thus research on single modalities in isolation results in missing much of the complexity inherent to communicative acts. Moreover, future studies of primate communication should adopt a multimodal, inclusive approach focusing on modalities in terms of both production and perception (Liebal et al. 2013; Fröhlich 2017). If primate communication is examined from the perspective of the signaler and signal form alone, researchers might fail to distinguish the proximate from the ultimate explanations for signals.



## Cross-References

- ▶ [Catarrhine Cognition](#)
- ▶ [Prosimian Communication](#)

## References

- Arbib, M. A., Liebal, K., & Pika, S. (2008). Primate vocalization, gesture, and the evolution of human language. *Current Anthropology*, *49*(6), 1053–1063.
- Barton, R. A. (2006). Olfactory evolution and behavioral ecology in primates. *American Journal of Primatology*, *68*(6), 545–558.
- Bradbury, J. W., & Vehrencamp, S. L. (1998). *Principles of animal communication*. Sunderland: Sinauer Associates.
- Call, J., & Tomasello, M. (2007). *The gestural communication of apes and monkeys*. Mahwah: Lawrence Erlbaum Associates.
- Crockford, C., & Boesch, C. (2005). Call combinations in wild chimpanzees. *Behaviour*, *142*, 397–421.
- Fedurek, P., Machanda, Z. P., Schel, A. M., & Slocombe, K. E. (2013). Pant hoot chorusing and social bonds in male chimpanzees. *Animal Behaviour*, *86*(1), 189–196.
- Fischer, J., & Zinner, D. (2011). Communication and cognition in primate group movement. *International Journal of Primatology*, *32*(6), 1279–1295.
- Freeberg, T. M., Dunbar, R. I. M., & Ord, T. J. (2012). Social complexity as a proximate and ultimate factor in communicative complexity. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *367* (1597), 1785–1801.
- Fröhlich, M., Wittig, R. M., & Pika, S. (2016). Play-solicitation gestures in chimpanzees in the wild: Flexible adjustment to social circumstances and individual matrices. *Royal Society Open Science*, *3*(8), 160278.
- Fröhlich, M. (2017). Taking turns across channels: Conversation-analytic tools in animal communication. *Neuroscience & Biobehavioral Reviews*.
- Geissmann, T., & Orgeldinger, M. (2000). The relationship between duet songs and pair bonds in siamangs, *Hylobates syndactylus*. *Animal Behaviour*, *60*(6), 805–809.
- Genty, E., Clay, Z., Hobaiter, C., & Zuberbühler, K. (2014). Multi-modal use of a socially directed call in bonobos. *PLoS One*, *9*(1), e84738.
- Ghazanfar, A. A., Takahashi, D. Y., Mathur, N., & Fitch, W. T. (2012). Cineradiography of monkey lip-smacking reveals putative precursors of speech dynamics. *Current Biology*, *22*(13), 1176–1182.
- Gouzoules, S., Gouzoules, H., & Marler, P. (1984). Rhesus monkey (*Macaca mulatta*) screams: Representational signalling in the recruitment of agonistic aid. *Animal Behaviour*, *32*(1), 182–193.
- Gruber, T., & Zuberbühler, K. (2013). Vocal recruitment for joint travel in wild chimpanzees. *PLoS One*, *8*(9), e76073.
- Higham, J. P., & Hebets, E. A. (2013). An introduction to multimodal communication. *Behavioral Ecology and Sociobiology*, *67*(9), 1381–1388.
- Higham, J. P., MacLarnon, A. M., Ross, C., Heistermann, M., & Semple, S. (2008). Baboon sexual swellings: Information content of size and color. *Hormones and Behavior*, *53*(3), 452–462.
- van Hooff, J. A. (1972). A comparative approach to the phylogeny of laughter and smiling. In R. A. Hinde (Ed.), *Non-verbal communication* (p. xiii, 443). Oxford: Cambridge University Press.
- Koda, H. (2004). Flexibility and context-sensitivity during the vocal exchange of coo calls in wild Japanese macaques (*Macaca fuscata yakui*). *Behaviour*, *141*, 1279–1296.
- Lemasson, A., Glas, L., Barbu, S., Lacroix, A., Guilloux, M., Remeuf, K., et al. (2011). Youngsters do not pay attention to conversational rules: Is this so for non-human primates? *Scientific Reports*, *1*, 22.
- Liebal, K., Waller, B. M., Burrows, A. M., & Slocombe, K. E. (2013). *Primate communication: A multimodal approach*. Cambridge: Cambridge University Press.
- Marler, P. (1965). Communication in monkeys and apes. In I. DeVore (Ed.), *Primate Behaviour: Field Studies of Monkeys and Apes*. (pp. 544–584). New York: Holt, Rinehart and Winston
- Matsumoto-Oda, A., Oda, R., Hayashi, Y., Murakami, H., Maeda, N., Kumazaki, K., et al. (2003). Vaginal fatty acids produced by chimpanzees during menstrual cycles. *Folia Primatologica*, *74*(2), 75–79.
- Nunn, C. L. (1999). The evolution of exaggerated sexual swellings in primates and the graded-signal hypothesis. *Animal Behaviour*, *58*(2), 229–246.
- Partan, S. R., & Marler, P. (2005). Issues in the classification of multimodal communication signals. *American Naturalist*, *166*(2), 231–245.
- Renoult, J. P., Schaefer, H. M., Sallé, B., & Charpentier, M. J. E. (2011). The evolution of the multicoloured face of mandrills: Insights from the perceptual space of colour vision. *PLoS One*, *6*(12), e29117.
- Rijksen, H. D. (1978). *A fieldstudy on Sumatran orangutans (Pongo pygmaeus abelii, Lesson 1827): Ecology, behaviour and conservation*. Wageningen: H. Veenman and Zonen.
- van Schaik, C. P., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, C. D., Singleton, I., et al. (2003). Orangutan cultures and the evolution of material culture. *Science*, *299*, 102–105.
- Semple, S., & Higham, J. P. (2013). Primate signals: Current issues and perspectives. *American Journal of Primatology*, *75*(7), 613–620.
- Setchell, J. M., & Jean Wickings, E. (2005). Dominance, status signals and coloration in male mandrills (*Mandrillus sphinx*). *Ethology*, *111*(1), 25–50.
- Smith, W. J. (1977). *The behavior of communicating: An ethological approach*. Cambridge, MA: Harvard University Press.
- Tomasello, M. (2008). *Origins of human communication*. Cambridge, MA: MIT Press.

- Tomasello, M., Call, J., Nagell, K., Olguin, R., & Carpenter, M. (1994). The learning and use of gestural signals by young chimpanzees: A trans-generational study. *Primates*, 35(2), 137–154.
- Vaglio, S., Minicozzi, P., Romoli, R., Boscaro, F., Pieraccini, G., Moneti, G., et al. (2016). Sternal gland scent-marking signals sex, age, rank, and group identity in captive mandrills. *Chemical Senses*, 41(2), 177–186.
- Van Hooff, J. A. R. A. M. (1967). The facial displays of the catarrhine monkeys and apes. In D. Morris (Ed.), *Primate ethology* (pp. 7–68). New Brunswick: AldineTransaction.
- Waller, B. M., & Micheletta, J. (2013). Facial expression in nonhuman animals. *Emotion Review*, 5(1), 54–59.
- Zuberbühler, K. (2001). Predator-specific alarm calls in Campbell's monkeys, *Cercopithecus campbelli*. *Behavioral Ecology and Sociobiology*, 50(5), 414–422.

# P

## Prosimian Diets

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Due to their smaller size, lower metabolic rates compared to haplorhines, and adaptation to vertical strata, prosimian diets are highly specialized and range between purely insectivorous and purely leaf eating. Sympatric *Cheirogaleus medius* and *C. major* have a diet of mostly fruits, followed by flowers, insects, and tree gums. Their foods are high in fiber, averaging 45.2% nitrogen detergent fiber (Lahann 2007). They reduce competition with other species by foraging at different heights with *C. medius* lower down and *C. major* higher up. Their diets are seasonal and select fruit during the weight gain season, to last through the following periods of hibernation. *Microcebus murinus* also has a varied diet of fruits, flowers, insects, and gums, which is highly seasonal and quite different depending on the field site (Dammhahn and Kappeler 2010; Lahann 2007). Gum is a major food source during particular seasons (Thoren et al. 2011). *Microcebus rufus*, being smaller in size, supports itself with fruits and insects and specifically the fruit of *Bakerella* spp. (Atsalis 1999). This is typical of many small-

sized prosimians. The smaller *Microcebus berthae* ingests a larger proportion of insects and also ingests insect secretions which reduce the seasonal fluctuation in diet (Dammhahn and Kappeler 2008). This technique is also employed by *Microcebus ravelobensis* which also ingests insects, gum, and fruit (Thoren et al. 2011). *Mirza* spp. are omnivorous and eat fruits, leaf buds, insects and their secretions, tree gums, and also some small vertebrates when available. *Allocebus* spp. are mostly insectivorous but were also observed licking twigs or bark which may have contained some sap, secretions, or exudates such as gum (Biebouw 2013). *Phaner* spp. are an extreme, ingesting mostly gum with a small compliments of insects (Charles-Dominique 1977). At another extreme is *Daubentoniidae madagascariensis* which ingests largely insects, specifically grubs, which it can find burrowed in tree trunks (Pollock et al. 1985). They also ingest some plant matter such as the fruit and seeds of *Canarium* spp.

The larger bodied lemurs also have varying and seasonal diets. *Indri indri* are folivorous; however, they have been observed ingesting some other plant parts depending upon their location and probably have an important amount of seed ingestion (Powzyk and Mowry 2003). Young leaves are around 73–80% of feeding time, 7% mature leaves, and 5–8% fruits and a combination of bark and petioles (Britt et al. 2002). Other leaf eaters include *Avahi laniger* and *A. meridionalis* which eat a mix of young and old leaves. *A.*

*meridionalis* are also able to diversify their diets to flowers during the growing season. Naturally, their diets are quite high in fiber which is similar throughout the prosimians (Norscica et al. 2012). *Avahi occidentalis* have a broader diet, feeding from 25 trees and 5 lianas, feeding on mostly leaves (77% of feeding time) with fruits and flowers also being eaten (Thalmann 2001). *Propithecus* spp. are similar, with *Propithecus diadema* being entirely plant eaters ingesting flowers (3–25%), fruits and seeds (22–65%), and young leaves (28–53%) (Overdorff and Strait 1998; Powzyk and Mowry 2003). *Propithecus verreauxi* and *Propithecus tattersalli* ingest between 25% and 46% leaves, 33% and 65% fruit, and 9–10% flowers based on feeding time (Richard 1978). The well-known *Lemur catta* are extensive generalists and opportunistic omnivores which spend equal time on fruits and leaves (Sauther et al. 1999). Specifically spending 25–58% of feeding time on leaves, 34–70% on fruits, and 2–8% of flowers with animal matter being ingested from time to time (Sussman 1974). *Eulemur* spp. are also generalists but supposedly described as frugivores. *Eulemur fulvus* ingests a diet of mostly leaves or fruits depending on the season (Sussman 1974). *Eulemur rubriventer* and *Eulemur coronatus* are much more frugivorous and only ingest up to 13.6% leaves with fruits sometimes being 100% of their foraging time (Overdorff and Strait 1998). *Eulemur macaco* and *Eulemur mongoz* have similar diets; however, only *E. mongoz* has been reported to ingest nectar more prominently (Colquhoun 1993). Similarly, *Varecia* spp. are largely fruit eaters with 70–90% of their diets being fruit, with leaves, flowers, and nectar being a seasonal part of their diet based upon availability (Ratsimbazafy 2002). The *Hapalemur* (*Hapalemur griseus*, *Hapalemur simus*, and *Hapalemur aureus*) are specialized on ingesting bamboo leaves, except for *H. aureus* which also enjoys foraging in reed beds (Eppley et al. 2011; Glander et al. 1989). Each species prefers different parts of the bamboo and some are specific for particular species. *H. griseus* ingests 88% bamboo and minor other grasses, preferring young leaf bases. *H. aureus* is similar, however prefers giant bamboo which is 78% of its feeding

time and some other bamboo species and fruits. The strictest diet is that of *H. simus*, with giant bamboo being 95% of the diet, eating both mature and immature leaves (Grassi 2001). *H. griseus* has been known to also ingest soil and fungi, with the diet being quite seasonal (Grassi 2001). Only *H. griseus alaotrensis* is described as eating 100% leaves (Randrianarisoa 1999). Other leaf eaters include the *Lepilemur* spp. which are less catholic in their choices of food than the previous Hapalemurs. Lepilemurs select their food based on the nutrient concentrations, allowing for a large variety of food items throughout the seasons (Thalmann 2001). *Lepilemur ruficaudatus* and *Lepilemur edwardsi* spend 75% of their foraging time on leaves and 25% on fruits, buds, and flowers, with coprophagy also having been observed (Thalmann 2001). Leaves were the main food of *Lepilemur leucopus*, spending 91% of its foraging time eating them and the rest on fruits, tree gum, and some bark.

The Lorisiform prosimians are generally smaller bodied and nocturnal. This allows for a specialized feeding of insects and tree gums, more so than any other mammalian group. With diets varying between insects, fruits, and gums, body size is generally able to dictate their general diet. Medium-sized *Perodicticus potto* are largely fruit eaters, while the smaller *Arctocebus calabarensis* are described as more insectivorous (Charles-Dominique 1977). This trend continues with the small-bodied *Loris* spp. who are either entirely insectivore (*Loris tardigradus*) or mostly insectivorous with minor amounts of gum and legume pods (*Loris lydekkerianus*) (Nekaris and Bearder 2007). This is to the contrary of the Asian slow lorises (*Nycticebus* spp.), which are largely exudativorous. The smallest *Nycticebus pygmaeus* has a diet of approximately 30% gum, 30% nectar, and 40% insects (Starr and Nekaris 2013). Their smaller size does not allow for sufficient fermentation of gums for their energy, insects and nectar are necessary for denser energy. The larger *Nycticebus coucang* has a more varied diet of fruits, insects, and tree gum in larger proportions than its smaller cousin (Wiens et al. 2006). The larger *Nycticebus javanicus* has a diet mostly of gum and insects, but also ingests a

small amount of fruits, nectar, flowers, and leaves which is a transition based on their larger body size (Cabana et al. 2017). The largest of the Asian slow lorises is *Nycticebus bengalensis*, which has a highly fermenting diet of 96% gum and some insects and leaves (Das et al. 2014).

The bushbabies are a group of nocturnal primates varied morphologically but also in size and ecology. The smaller *Galago zanzibaricus* and *Galago senegalensis* are largely insectivorous, ingesting up to 70% insects, with some fruit and gum (Harcourt and Nash 1986). Gum is particularly important to the diet of *G. senegalensis* which can feed on it for up to 30% of its feeding time. This is similar to *G. moholi* which spends up to 48% of their time on gum and 50% on insects (Nekaris and Bearder 2007). The larger *Otolemur garnettii* and *Otolemur crassicaudatus* are able to ingest more gum (40%) and insects (40%) due to their size, with *O. garnettii* also relying on seasonal fruits (Harcourt and Nash 1986; Nekaris and Bearder 2007). Depending on the field site, *O. garnettii* was also described as highly insectivorous, having a diet 50–55% of animal matter, specifically insects and molluscs (Masters et al. 1988). The *Galagoides demodivii* and *cocos* have a highly insectivorous diet of 70% insects and 30% fruits (Charles-Dominique 1977; Nekaris and Bearder 2007). *Galagoides alleni* spent its time equally on animal matter and fruit. *Euoticus elegantulus* is the most exudativorous of the bushbabies, with only 20% of time spent on animal matter.

All of the diet information reported in this chapter is based on the percentage of time spent on foraging or feeding, therefore the percentages reported do not directly reflect the intake. Especially for insects and nectar, the ingested amount is often much lower than the feeding percentage and fruits tends to be higher (Cabana et al. 2017).

## Cross-References

- ▶ [Cattarrhine Diet](#)
- ▶ [Dentition](#)
- ▶ [Digestive System](#)
- ▶ [Feeding](#)

- ▶ [Geophagy](#)
- ▶ [Hominoidea Diet](#)
- ▶ [Jarman/Bell Principle](#)
- ▶ [Platyrrhine Diet](#)
- ▶ [Primate Diet](#)
- ▶ [Prosimian Life History](#)
- ▶ [Prosimian Morphology](#)
- ▶ [Protein](#)

## References

- Atsalis, S. (1999). Diet of the brown mouse lemur (*Microcebus rufus*) in Ranomafana National Park, Madagascar. *International Journal of Primatology*, 20, 193–229.
- Biebouw, K. (2013). Preliminary results on the behavioural ecology of the hairy-eared dwarf lemur (*Allocebus trichotis*) in Andasibe, eastern Madagascar. In J. Masters, M. Gamba, & F. Genin (Eds.), *Leaping ahead: Advances in prosimian biology* (pp. 253–275). New York: Springer.
- Britt, A., Randriamandratonirina, N. J., Glasscock, K. D., & Iambana, B. R. (2002). Diet and feeding behavior of *Indri indri* in a low-altitude rain forest. *Folia Primatologica*, 73, 225–239.
- Cabana, F., Dierenfeld, E., Wirdateti, W., Donati, G., & Nekaris, K. A. I. (2017). The seasonal feeding ecology of the Javan slow loris (*Nycticebus javanicus*). *American Journal of Physical Anthropology*, 162, 768–781.
- Charles-Dominique, P. (1977). Ecology and behaviour of nocturnal primates: prosimians of equatorial West Africa. Columbia University Press.
- Colquhoun, I. C. (1993). The socioecology of *Eulemur macaco*: A preliminary report. In P. M. Kappeler & J. U. Ganzhorn (Eds.), *Lemur social systems and their ecological basis* (pp. 11–24). New York: Plenum Press.
- Dammhahn, M., & Kappeler, P. M. (2008). Comparative feeding ecology of sympatric *Microcebus berthae* and *M. murinus*. *International Journal of Primatology*, 29, 1567–1589.
- Dammhahn, M., & Kappeler, P. M. (2010). Scramble or contest competition over food in solitary foraging mouse lemurs (*Microcebus* spp.): New insights from stable isotopes. *American Journal of Physical Anthropology*, 141, 181–189.
- Das, N., Nekaris, K. A. I., & Bhattacharjee, P. C. (2014). Medicinal plant exudativory by the Bengal slow loris *Nycticebus bengalensis*. *Endangered Species Research*, 23, 149–157.
- Eppley, T. M., Verjans, E., & Donati, G. (2011). Coping with low-quality diets: A first account of the feeding ecology of the southern gentle lemur, *Hapalemur meridionalis*, in the Mandena littoral forest, southeast Madagascar. *Primates*, 52, 7–13.
- Glander, K. E., Wright, P. C., Seigler, D. S., Randrianasolo, V., & Randrianasolo, B. (1989). Consumption of



- cyanogenic bamboo by a newly discovered species of bamboo lemur. *American Journal of Primatology*, 19, 119–124.
- Grassi, C. (2001). The behavioral ecology of *Hapalemur griseus griseus*: The influences of microhabitat and population density on this small-bodied prosimian folivore (Madagascar) (Ph.D. Dissertation). University of Texas, Austin.
- Harcourt, C. S., & Nash, L. T. (1986). Species differences in substrate use and diet between sympatric galagos in two Kenyan coastal forests. *Primates*, 27, 41–52.
- Lahann, P. (2007). Feeding ecology and seed dispersal of sympatric cheirogaleid lemurs (*Microcebus murinus*, *Cheirogaleus medius*, *Cheirogaleus major*) in the littoral rainforest of south-east Madagascar. *Journal of Zoology*, 271, 88–98.
- Masters, J. C., Lumsden, W. H. R., & Young, D. A. (1988). Reproductive and dietary parameters in wild greater galago populations. *International Journal of Primatology*, 9, 573–592.
- Nekaris, K. A. I., & Bearder, S. K. (2007). The Lorisiform primates of Asia and mainland Africa. In C. Campbell, A. Fuentes, K. Mackinnon, S. K. Bearder, & R. Stumpf (Eds.), *Primates in perspective* (pp. 24–45). New York: Oxford University Press.
- Norscica, I., Ramanamanjato, J. B., & Ganzhorn, J. U. (2012). Feeding patterns and dietary profile of nocturnal southern woolly lemurs (*Avahi meridionalis*) in Southeast Madagascar. *International Journal of Primatology*, 33, 150–167.
- Overdorff, D. J., & Strait, S. G. (1998). Seed handling by three prosimian primates in southeastern Madagascar: Implications for seed dispersal. *American Journal of Primatology*, 45, 69–82.
- Pollock, J. I., Constable, I. D., Mittermeier, R. A., Ratsirarson, J., & Simons, H. (1985). A note on the diet and feeding behavior of the aye-aye *Daubentonia madagascariensis*. *International Journal of Primatology*, 6, 435–447.
- Powzyk, J. A., & Mowry, C. B. (2003). Dietary and feeding differences between sympatric *Propithecus diadema diadema* and *Indri indri*. *International Journal of Primatology*, 24, 1143–1162.
- Randrianarisoa, A. J. (1999). Estimation of food intake in wild Alaotran gentle lemurs *Hapalemur griseus alaotrensis*. *Dodo*, 35, 171.
- Ratsimbazafy, J. H. (2002). *On the brink of extinction and the process of recovery: Responses of black-and-white ruffed lemurs (Varecia variegata variegata) to habitat disturbance in Manombo* (Ph.D. Dissertation). Stony Brook University, Stony Brook.
- Richard, A. F. (1978). Variability in the feeding behavior of a Malagasy prosimian, *Propithecus verreauxi*: Lemuriformes. In *The ecology of arboreal folivores* (pp. 519–533). Washington, DC: Smithsonian Institution Press.
- Sauther, M. L., Sussman, R. W., & Gould, L. (1999). The socioecology of the ringtailed lemur: Thirty-five years of research. *Evolutionary Anthropology*, 8, 120–132.
- Starr, C., & Nekaris, K. A. I. (2013). Obligate exudativory characterizes the diet of the pygmy slow loris *Nycticebus pygmaeus*. *American Journal of Primatology*, 75, 1054–1061.
- Sussman, R. W. (1974). Ecologie de 2 espèces coexistantes de Lémur *Lemur catta* et *Lemur fulvus rufus*. *Bulletin de l'Académie Malgache*, 52, 175–191.
- Thalmann, U. (2001). Food resource characteristics in two nocturnal lemurs with different social behavior: *Avahi occidentalis* and *Lepilemur edwardsi*. *International Journal of Primatology*, 22, 287–324.
- Thoren, S., Quitzsh, F., Schwochow, D., Sehen, L., Meusel, C., Meares, K., & Radespiel, U. (2011). Seasonal changes in feeding ecology and activity patterns of two sympatric mouse lemur species, the gray mouse lemur (*Microcebus murinus*) and the golden-brown mouse lemur (*M. ravelobensis*), in Northwestern Madagascar. *International Journal of Primatology*, 32, 566–586.
- Wiens, F., Zitzmann, A., & Hussein, N. A. (2006). Fast food for slow lorises: Is low metabolism related to secondary compounds in high-energy plant diet? *Journal of Mammalogy*, 87, 790–798.

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## Prosimian Communication

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### Synonyms

[Galago](#); [Lemur](#); [Loris](#); [Olfaction](#); [Scent mark](#); [Strepsirrhine](#); [Tarsier](#); [Vocalization](#)

### Introduction

Prosimians are a group of primates which include lemurs, galagos, lorises, and tarsiers. They are diverse in their social systems, activity periods, and habitats. They may live in groups or forage solitarily, be diurnal or nocturnal, and live in diverse environments. They have complex, multimodal communication systems which rely heavily on auditory (vocalizations), olfactory (scent marks), and visual signals (movements and fur markings). These signaling modalities enable prosimians to communicate at various distances during both day and night and through different types of habitat. Both vocalizations and scent can be used to communicate between individuals that are near or far. Soft vocalizations are used for close range, and loud calls are used for distant individuals. Similarly, scent can be perceived by nearby individuals, or scent marks can be deposited to be detected by others long after the

individual that produced it has moved away. Movement and fur color patterns are used to communicate at distances that are close enough for visual contact. These various communication modalities combine to enable prosimians discern information about an individual, potentially including species, individual identity, sex, reproductive status, and kinship relationships. Prosimians communicate while engaging in complex social interactions including maintaining ranges, attracting and searching for mates, and raising young.

### Vocalizations

The auditory channel is an important part of prosimian communication and the primary method of signaling is through vocalizations. Prosimian vocalizations vary greatly across species in acoustic range and usage. Most species vocalize in the range that is audible to humans (up to ~20,000 Hz), but a few species also have vocalizations which are either partially (mouse lemurs) or entirely (tarsiers) in the ultrasonic range (Ramsier et al. 2012; Zimmermann 1995). Because such ranges are above the hearing range of predatory birds, this is thought to be an adaptation for avoiding eavesdropping by predators (Ramsier et al. 2012; Zimmermann 1995).

Vocalizations have been shown to convey a great deal of information about the caller including species, sex, individual identity, and even kin

group (citations below). Source-filter theory (Fant 1960) explains how such information is detectable in vocalizations. The source of the sound is air passing through the animal's vocal folds. The rate at which the vocal folds vibrate determines how high or low the sound is. Then as the sound waves pass through the vocal tract and out the mouth, different frequencies are amplified or dampened due to the morphology of the vocal tract. Because an individual's vocal tract morphology may vary according to its species, sex, individual identity, and kin group, this can produce voices that are distinctive by species, sex, individual identity, and kin group.

Of the prosimians, the lemurs are probably the most intensively studied. This research has shown that various lemur species have calls that are distinctive by species (sportive lemurs: (Méndez-Cárdenas et al. 2008), true lemurs: (Gamba et al. 2012b)), sex (sifakas: (Patel and Owren 2012)), individual identity (sifakas: (Patel and Owren 2012), red-bellied lemurs: (Gamba et al. 2012a), mouse lemurs: (Leliveld et al. 2011)), and kin group (mouse lemurs: (Kessler et al. 2014; Kessler et al. 2012)). Similarly, galago calls have been argued to be distinctive by individual (Kessler et al. 2015) and species (Anderson et al. 2000). In comparison, much less research has been done on the vocalizations of the lorises and tarsiers, though vocalizations are increasingly used in species identification among the tarsiers (Burton and Nietsch 2010).

Research into the acoustic variations between individuals, populations, and species is currently under intense interest for its potential applications to conservation as a tool for identifying species and developing acoustic monitoring programs (Burton and Nietsch 2010). Such programs would enable conservationists to obtain a great deal of information about how these species – many of which are small, cryptic, nocturnal, and difficult to follow – use the forest without trapping them or disturbing them.

However, from the perspective of animal communication, it is important to distinguish between when the variability exists to statistically distinguish between species, individuals, sexes, or kin groups and whether the animals actually detect

and use this information. This requires the use of playback experiments. During playback experiments, recordings of vocalizations are played, and the subjects' behavioral responses, like whether they look toward the loudspeaker, are measured. Playback studies have been used to show that prosimians may detect when vocalizations vary by species (mouse lemurs: (Braune et al. 2008)), individual identity (Kulahci et al. 2014), and kin group (mouse lemurs: (Kessler et al. 2012), ring-tailed lemurs: (Nunn 2000)).

Prosimians use vocalizations to communicate in many different social contexts. This includes both species that live in cohesive social groups and solitary foraging species. Vocalizations can be given as coordinated vocal displays, like the duets of sportive lemurs (Méndez-Cárdenas and Zimmermann 2009) and tarsiers (Burton and Nietsch 2010) or the loud group choruses given by Indri groups when engaging in territorial displays (Torti et al. 2012). Alternatively, vocalizations may be given without being part of a coordinated display but may still have important roles in social bonding (ring-tailed lemurs (Kulahci et al. 2015)), defense against predators (mouse lemurs (Eberle and Kappeler 2008), sifaka and red-fronted lemurs (Fichtel 2004), tarsiers (Gursky 2006)), maintaining spacing between individuals and group coordination (mouse lemurs (Braune et al. 2005), red-fronted lemurs (Pflueger and Fichtel 2012)), mate advertisement and territory defense (sportive lemurs (Seiler et al. 2015)), and rearing young (bush babies (Becker et al. 2003), mouse lemurs (Scheumann et al. 2007)).

## Scent Marking

Prosimians rely more on olfactory communication than do other primates. They are believed to have functional vomeronasal organs that help them to detect olfactory cues (Smith et al. 2015). Prosimians use several types of scent marks including latrines, fecal marking, urine marking, and/or urine washing (when the animal urinates on its own hands and feet, and then deposits the urine from the hands and feet as it travels), as well as marking using scent from the chin, forehead,

palms, genitals, or specialized scent glands (Delbarco-Trillo et al. 2011). Sources of the scent may include feces, urine, saliva, sweat, skin, or secretions from glands in the genital, perianal, gular, sternal, brachial, or antebrachial regions (Delbarco-Trillo et al. 2011; delBarco-Trillo et al. 2012). Some species also mix scents from more than one source before depositing it (Greene et al. 2016).

Because much less is known about olfactory communication than vocal communication, studies comparing olfactory communication across prosimian species are still relatively rare. However, there have been a few studies which have begun to illuminate how olfactory communication has evolved in prosimians. Urine marking has been reconstructed as one of the oldest forms and is the main form of scent marking used by nocturnal, solitary foraging species such as the galagos, lorises, and several nocturnal lemurs (Delbarco-Trillo et al. 2011). Such urine marking may also take the form of urine washing. In general, these predominantly urine-marking species have more chemically complex urine, meaning that the urine contains more different compounds, than species which do not mark with urine (Delbarco-Trillo et al. 2011). The evolutionary shift from urine marking in nocturnal, solitary foragers to depositing scent from scent glands in cathemeral and diurnal species is believed to have evolved due to the increasing social complexity in these species (Delbarco-Trillo et al. 2011). These species forage in cohesive social groups; thus, these marks may be important for both intragroup and intergroup communication (Delbarco-Trillo et al. 2011). Glandular scent marks can be highly complex relative to urine (Delbarco-Trillo et al. 2011). For example, the number of compounds found in urine ranged from 2 to 33, while ring-tailed lemurs may express 200 to 300 different compounds in their glandular secretions (Delbarco-Trillo et al. 2011).

This relationship between social complexity and chemical complexity in scent marks was also supported in a study comparing scent-mark chemistry and degree of sociality between eight *Eulemur* species (delBarco-Trillo et al. 2012). These species live in cohesive social groups with

differing social organizations (pair-bonded or multi-male multi-female) and differing dominance relations between the sexes (female dominant or codominant). Interestingly, differences associated with social system and dominance relationships between the sexes were found (delBarco-Trillo et al. 2012). Female scent marks were chemically more complex in species that live in multi-male, multi-female groups relative to the marks of females of pair-bonded species (delBarco-Trillo et al. 2012). Similarly, male scent marks were more complex in species where males are codominant with females relative to the marks of males in female-dominant species (delBarco-Trillo et al. 2012). When the sexes were compared, males in codominant species had more complex scent marks relative to females in the same species (delBarco-Trillo et al. 2012). However, in female-dominant species, the females had more complex signals relative to the males (delBarco-Trillo et al. 2012).

Much less is known about the signal content of scent marks relative to vocalizations, but it is an area that is receiving a lot of research. So far, scent marks appear to have the potential to reveal a lot of information about the individual that placed the mark. Lemurs have received the most research with studies showing that sifaka secretions signal sex, season, and genetic relatedness, meaning that the signals of closely related individuals are more similar than those of more distantly related individuals (Morelli et al. 2014). Similarly, ring-tailed lemurs secrete scents which vary by individual (Scordato et al. 2007), season (Scordato et al. 2007), and genetic relatedness (Boulet et al. 2009). Scent signals appear to be important for mate choice. Male ring-tailed lemur scent marks have been shown to convey information on genome-wide heterozygosity of the signaler, which itself correlates with health and survivorship, making it a useful signal for mate choice (Charpentier et al. 2008). Female signals also provide important information, varying according to whether they are pregnant (Crawford and Drea 2015) or on hormonal contraception (Crawford et al. 2011). Relative to the lemurs, much less work has been done on the other prosimians species. Early work on greater galagos showed that thick-

tailed galagos use scent marks to discriminate between the sexes, evaluate reproductive state (Clark 1982a), and differentiate between individuals (Clark 1982b). Both thick-tailed galagos and Garnett's greater bush baby discriminated between their own and the other species (Clark 1988).

While the above studies largely focused on the information content of scent marks, either through examining whether the chemical composition varies by individual, species, etc. or by examining whether the animals respond differently to scents from different individuals, species, etc., another subset of studies has begun to investigate the how scent marks are used. For example, recent work has shown that wild spectral tarsiers scent mark primarily for territory defense, not to monitor the reproductive state of females (Gursky-Doyen 2010). Tarsiers marked most often along territory borders, more frequently on nights with territory disputes, and more often during the dry season when resources were scarcer than in the wet season (Gursky-Doyen 2010). They did not mark more often during the mating season than the non-mating season (Gursky-Doyen 2010) as would be expected if scent marks were used to monitor female reproductive state. Similarly, mouse lemurs are more likely to scent mark when leaving a sleeping site than when reuniting at a sleeping site suggesting that the marks were important for maintaining spacing between sleeping groups and access to sleeping sites (Braune et al. 2005).

Interestingly, the slow lorises also secrete chemicals, but these secretions are specialized for defense (Nekaris et al. 2013). The loris mixes oil from its brachial arm glands with saliva to produce venom which it rubs on its own fur (Nekaris et al. 2013). This venom is strong enough to induce shock and death in small mammals (Nekaris et al. 2013). The main functions are thought to be for defense against parasites and other lorises (Nekaris et al. 2013).

## Multimodal Communication

While most work on prosimians communication has focused on vocalizations and scent marks individually, recent work has emphasized that

these modalities work together. For example, ring-tailed lemurs were shown to be able to match the scents and vocalizations of individuals (Kulahci et al. 2014). Similarly, not only do species using glandular scent marks emit olfactory signals, but these signals are also multimodal (Scordato et al. 2007). The individual depositing them often does so with conspicuous visual or auditory cues (Scordato et al. 2007). Visual cues include handstands to deposit anogenital marks or elaborate movements such as the ring-tailed "stink fights" in which males anoint their tails with brachial and antebrachial secretions and then wave their tails at each other (Scordato et al. 2007). Auditory cues include scratching tree bark with an antebrachial spur during deposition (Scordato et al. 2007). Other group-mates may respond to this multimodal signal by investigating and adding marks of their own. Similar opportunities for combining sensor modalities occur when vocalizations or scent marks are paired with individually or species specific face markings, such as those occurring in several species of loris (Nekaris and Munds 2010) and galago (Bearder 1999).

## Conclusion

Prosimians have multimodal communication systems in which they combine auditory, olfactory, and visual signals to convey information about who they are and to navigate social interactions. These communication systems are complex enough to communicate information about their species, sex, individual identity, kin group, and reproductive status during interactions relating to dominance, territorial displays, mate choice, and raising young. These signals are also flexible to enable communication during day or night, through dense forest, and to individuals both within a cohesive social group and to others in a dispersed social network.

## Cross-References

- ▶ [Primate Cognition](#)
- ▶ [Primate Communication](#)



- ▶ Primate Sensory Systems
- ▶ Primate Social Structure

## References

- Anderson, M. J., Ambrose, L., Bearder, S. K., Dixon, A. F., & Pullen, S. (2000). Intraspecific variation in the vocalizations and hand pad morphology of southern lesser bush babies (*Galago moholi*): A comparison with *G. senegalensis*. *International Journal of Primatology*, 21(3), 537–555.
- Bearder, S. K. (1999). Physical and social diversity among nocturnal primates: A new view based on long term research. *Primates*, 40(1), 267–282.
- Becker, M., Buder, E., Bakeman, R., Price, M., & Ward, E. (2003). Infant response to mother call patterns in *Otolemur garnettii*. *Folia Primatol (Basel)*, 74(5–6), 301–311.
- Boulet, M., Charpentier, M. J. E., & Drea, C. M. (2009). Decoding an olfactory mechanism of kin recognition and inbreeding avoidance in a primate. *BMC Evolutionary Biology*, 9, 281.
- Braune, P., Schmidt, S., & Zimmermann, E. (2005). Spacing and group coordination in a nocturnal primate, the golden brown mouse lemur (*Microcebus ravelobensis*): The role of olfactory and acoustic signals. *Behavioral Ecology and Sociobiology*, 58(6), 587–596.
- Braune, P., Schmidt, S., & Zimmermann, E. (2008). Acoustic divergence in the communication of cryptic species of nocturnal primates (*Microcebus* spp.) *BMC Biology*, 6, 19.
- Burton, J. A., & Nietsch, A. (2010). Geographical variation in duet songs of Sulawesi tarsiers: Evidence for new cryptic species in south and southeast Sulawesi. *International Journal of Primatology*, 31(6), 1123–1146.
- Charpentier, M. J. E., Boulet, M., & Drea, C. M. (2008). Smelling right: The scent of male lemurs advertises genetic quality and relatedness. *Molecular Ecology*, 17(14), 3225–3233.
- Clark, A. B. (1982a). Scent marks as social signals in *Galago crassicaudatus*. I. Sex and reproductive status as factors in signals and responses. *Journal of Chemical Ecology*, 8(8), 1133–1151.
- Clark, A. B. (1982b). Scent marks as social signals in *Galago crassicaudatus*: II. Discrimination between individuals by scent. *Journal of Chemical Ecology*, 8(8), 1153–1165.
- Clark, A. B. (1988). Interspecific differences and discrimination of auditory and olfactory signals of *Galago crassicaudatus* and *Galago garnettii*. *International Journal of Primatology*, 9(6), 557–571.
- Crawford, J. C., & Drea, C. M. (2015). Baby on board: Olfactory cues indicate pregnancy and fetal sex in a non-human primate. *Biology Letters*, 11(2), 5.
- Crawford, J. C., Boulet, M., & Drea, C. M. (2011). Smelling wrong: Hormonal contraception in lemurs alters critical female odour cues. *Proceedings of the Royal Society B: Biological Sciences*, 278(1702), 122–130.
- DelBarco-Trillo, J., Burkert, B. A., Goodwin, T. E., & Drea, C. M. (2011). Night and day: The comparative study of strepsirrhine primates reveals socioecological and phylogenetic patterns in olfactory signals. *Journal of Evolutionary Biology*, 24(1), 82–98.
- delBarco-Trillo, J., Sacha, C. R., Dubay, G. R., & Drea, C. M. (2012). Eulemur, me lemur: The evolution of scent-signal complexity in a primate clade. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 367(1597), 1909–1922.
- Eberle, M., & Kappeler, P. M. (2008). Mutualism, reciprocity, or kin selection? Cooperative rescue of a conspecific from a boa in a nocturnal solitary forager the gray mouse lemur. *American Journal of Primatology*, 70(4), 410–414.
- Fant, G. (1960). *Acoustic theory of speech production*. The Hague: Mouton & Co. N. V., Publishers.
- Fichtel, C. (2004). Reciprocal recognition of sifaka (*Propithecus verreauxi verreauxi*) and redfronted lemur (*Eulemur fulvus rufus*) alarm calls. *Animal Cognition*, 7(1), 45–52.
- Gamba, M., Colombo, C., & Giacoma, C. (2012a). Acoustic cues to caller identity in lemurs: A case study. *Journal of Ethology*, 30(1), 191–196.
- Gamba, M., Friard, O., & Giacoma, C. (2012b). Vocal tract morphology determines species-specific features in vocal signals of lemurs (*Eulemur*). *International Journal of Primatology*, 33(6), 1453–1466.
- Greene, L. K., Grogan, K. E., Smyth, K. N., Adams, C. A., Klager, S. A., & Drea, C. M. (2016). Mix it and fix it: Functions of composite olfactory signals in ring-tailed lemurs. *Royal Society Open Science*, 3(4), 10.
- Gursky, S. (2006). Function of snake mobbing in spectral tarsiers. *American Journal of Physical Anthropology*, 129(4), 601–608.
- Gursky-Doyen, S. (2010). The function of scent-marking in spectral tarsiers. In S. Gursky-Doyen & J. Supriatna (Eds.), *Indonesian Primates* (pp. 359–369). New York: Springer.
- Kessler, S. E., Scheumann, M., Nash, L. T., & Zimmermann, E. (2012). Paternal kin recognition in the high frequency/ultrasonic range in a solitary foraging mammal. *BMC Ecology*, 12, 26.
- Kessler, S. E., Radespiel, U., Hasiniaina, A., Leliveld, L., Nash, L. T., & Zimmermann, E. (2014). Modeling the origins of mammalian sociality: Moderate evidence for matrilineal signatures in mouse lemur vocalizations. *Frontiers in Zoology*, 11, 14.
- Kessler, S. E., Scheumann, M., Hanbury, D. B., Nash, L. T., Zimmermann, E., & Watson, S. L. (2015). Screams in the night: Pilot study reveals moderate evidence for individual differences in loroid vocalizations. *International Journal of Primatology*, 36(3), 666–678.
- Kulahci, I. G., Drea, C. M., Rubenstein, D. I., & Ghazanfar, A. A. (2014). Individual recognition through olfactory – Auditory matching in lemurs. *Proceedings of the Royal Society B: Biological Sciences*, 281(1784), 6.

- Kulahci, I. G., Rubenstein, D. I., & Ghazanfar, A. A. (2015). Lemurs groom-at-a-distance through vocal networks. *Animal Behaviour*, *110*, 179–186.
- Leliveld, L. M. C., Scheumann, M., & Zimmermann, E. (2011). Acoustic correlates of individuality in the vocal repertoire of a nocturnal primate (*Microcebus murinus*). *The Journal of the Acoustical Society of America*, *129*(4), 2278–2288.
- Méndez-Cárdenas, M. G., & Zimmermann, E. (2009). Duetting-a mechanism to strengthen pair bonds in a dispersed pair-living primate (*Lepilemur edwardsi*)? *American Journal of Physical Anthropology*, *139*(4), 523–532.
- Mendez-Cárdenas, M., Randrianambinina, B., Rabesandratana, A., Rasoloharijaona, S., & Zimmermann, E. (2008). Geographic variation in loud calls of sportive lemurs (*Lepilemur* spp.) and their implications for conservation. *American Journal of Primatology*, *70*(9), 828–838.
- Morelli, T. L., Hayes, R. A., Nahrung, H. F., Goodwin, T. E., Harelimana, I. H., MacDonald, L. J., et al. (2014). Relatedness communicated in lemur scent. *Naturwissenschaften*, *100*(8), 769–777.
- Nekaris, K. A. I., & Munds, R. (2010). Using facial markings to unmask diversity: The slow lorises (primates: Lorisidae: *Nycticebus*) of Indonesia. In S. Gursky & J. Supriatna (Eds.), *Indonesian Primates* (pp. 383–396). New York: Springer.
- Nekaris, K. A.-I., Moore, R. S., Rode, E. J., & Fry, B. G. (2013). Mad, bad and dangerous to know: The biochemistry, ecology and evolution of slow loris venom. *The Journal of Venomous Animals and Toxins Including Tropical Diseases*, *19*, 21–21.
- Nunn, C. L. (2000). Maternal recognition of infant calls in ring-tailed lemurs. *Folia Primatol (Basel)*, *71*(3), 142–146.
- Patel, E. R., & Owren, M. J. (2012). Silky sifaka (*Protopithecus candidus*) “zzuss” vocalizations: Sexual dimorphism, individuality, and function in the alarm call of a monomorphic lemur. *The Journal of the Acoustical Society of America*, *132*(3), 1799–1810.
- Pflueger, F. J., & Fichtel, C. (2012). On the function of redfronted lemurs’ close calls. *Animal Cognition*, *15*(5), 823–831.
- Ramsier, M. A., Cunningham, A. J., Moritz, G. L., Finneran, J. J., Williams, C. V., Ong, P. S., et al. (2012). Primate communication in the pure ultrasound. *Biology Letters*, *8*(4), 508–511.
- Scheumann, M., Zimmermann, E., & Deichsel, G. (2007). Context-specific calls signal infants’ needs in a strepsirrhine primate, the gray mouse lemur (*Microcebus murinus*). *Developmental Psychobiology*, *49*(7), 708–718.
- Scordato, E. S., Dubay, G., & Drea, C. M. (2007). Chemical composition of scent marks in the ringtailed lemur (*Lemur catta*): Glandular differences, seasonal variation, and individual signatures. *Chemical Senses*, *32*(5), 493–504.
- Seiler, M., Schwitzer, C., & Holderied, M. (2015). Call repertoire of the Sahamalaza sportive lemur, *Lepilemur sahalazensis*. *International Journal of Primatology*, *36*(3), 647–665.
- Smith, T. D., Muchlinski, M. N., Bhatnagar, K. P., Durham, E. L., Bonar, C. J., & Burrows, A. M. (2015). The vomeronasal organ of *Lemur catta*. *American Journal of Primatology*, *77*(2), 229–238.
- Torti, V., Gamba, M., Rabemananjara, Z. H., & Giacoma, C. (2012). The songs of the indris (Mammalia: Primates: Indridae): Contextual variation in the long-distance calls of a lemur. *Italian Journal of Zoology*, *80*(4), 596–607.
- Zimmermann, E. (1995). Acoustic communication in nocturnal prosimians. In L. Alterman, G. A. Doyle, & M. K. Izard (Eds.), *Creatures of the dark* (pp. 311–330). New York: Plenum Press.

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## Catarrhine Diet

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### Introduction

Most primates are morphologically and physiologically adapted as frugivores and seek out energy and nutrient-dense foods. Primates have long periods of gestation and nursing and have high encephalization quotients (brain to body ratio), thus requiring large amounts of energy to function properly. The energetic demands of primates' large brains alone require daily consumption of large amounts of energy-rich foods (Aiello and Wheeler 1995).

Within the diverse parvorder *Catarrhini* (which encompasses old-world monkeys, apes, and humans), there is a great deal of dietary variability, ranging in degree of folivory (leaf eating), frugivory (fruit eating), granivory (seed eating), and graminivory (grass eating). Lambert and Rothman (2015) state that most primate species are in fact what they call “flexible omnivores,” meaning that not only do primate species switch between different food sources, but that the foods themselves (both food type and nutrient composition) vary based on location, seasonality, and time of day. Even among many of the catarrhine species who are classified under the dietary categories

of “folivore” or “frugivore,” there is still a great deal of dietary variability. It should be noted that even with this dietary flexibility, there are still a few primates that will preferentially select, and are specialized for, certain types of foods (i.e., leaf-eating colobines, grass-eating gelada baboons, etc.). Additionally, within all primate species, the use of fallback foods, or foods that are eaten when preferred foods are unavailable, is regularly observed. Moreover, large-bodied primates, such as catarrhine species, serve a vital role as seed dispersers which aid in the development and maintenance of the ecosystems and habitats (primarily forested areas) in which they live.

### Old-World Monkeys

The largest group, with the most species within *Catarrhini*, is the old-world monkeys. Old-world monkeys range throughout the continents of Asia and Africa (and one species in South Europe), are typically larger bodied than their New World counterparts, and are generally flexible feeders. Within the old-world monkeys are the two sub-families Colobinae (African and Asian colobines) and Cercopithecinae (cheek-pouched monkeys).

### Colobines

Colobines are also known as the “leaf-eating” monkeys, though their diet is much more complex and varied (Fashing 2011; Kirkpatrick 2011). All colobines have specialized multi-chambered or

sacculated stomachs that allow for fermentation of high-fiber foods (Kay and Davies 1994). This fermentation process also helps to detoxify plants and is achieved by the symbiotic relationship with species-specific microbiota that live in their intestines. This ability to ferment low-quality foods, such as mature leaves, allows for colobines to survive on a diet many other animals could not. Moreover, all colobine species have adaptations in addition to sacculated stomachs that allow them to process leaves including enlarged salivary glands and molars capable of processing tough plant foods. Colobines tend to prefer young leaves and fruit to mature leaves but will forage and feed on mature leaves when necessary.

*Asian colobines:* Asian colobines have, according to Kirkpatrick (2011), diets that vary by season and include leaves, fruits, and seeds. While most Asian colobines' diet is primarily leaves, Kirkpatrick (2011) states that about a quarter of their diet consists of fruits and seeds, and while invertebrate consumption is rare, it does occur (Newton 1992).

*African colobines:* Like their Asian counterparts, African colobines are leaf-eating monkeys. However, similar to the Asian colobines, their diet does alter seasonally, and fruit, seed, and flower consumption is regularly observed. While some of the larger-bodied African colobines don't have a problem relying on mature leaves when other food sources aren't available, some of the smaller-bodied species might not be able to ingest such low-quality foods.

### **Cercopithecines**

The cercopithecines span both the continents of Asia and Africa (and one macaque species in Gibraltar). These primates, which share morphological characteristics of cheek pouches and ischial callosities (thick-callused pads on the buttocks), include African papionins (baboons, gelada baboons, mangabeys, mandrills, drills), macaques (the most successful primate species, second only to humans), guenons, and vervets. Save the gelada baboon, cercopithecines are largely flexible omnivores, though like all other

primates, foods are chosen based on nutrient content.

*Baboons and Baboon-Like Primates* Baboons (*Papio* sp.) eat a wide variety of foods and are considered opportunistic omnivores. As they are the most widely disbursed primate in Africa, troop diets may vary depending on location. For example, baboons who live near the ocean have been observed eating and foraging for shellfish and mermaid's purses (shark eggs), while some baboons who live near soda lakes hunt for flamingo. Many of these foraging strategies are culturally passed from generation to generation. Additionally, they use their short, dexterous fingers to dig for underground storage organs and feed on flowers, fruits, gums, seeds, leaves, grasses, and various animal prey. Baboons tend to choose diets that are low in fiber, high in protein, and high in fat. As baboons are capable of a great deal of dietary flexibility and as human and baboon populations continue to collide, baboons have begun foraging in trash heaps, crops, and settlements.

One interesting and specialized cercopithecine that is commonly referred to as a baboon, though not a member of the genus *Papio*, is the gelada baboon (*Theropithecus gelada*). Gelada baboons are grass specialists (graminivores) who spend their days foraging on the grasses in the highlands of Ethiopia, the only place in the world where they are found. Because they spend their days foraging on grasses and sitting down, some interesting behavioral and morphological adaptations have emerged. Behaviorally, gelada "chatter" or verbally groom one another throughout the day, as they don't have the time to physically groom one another. Morphologically, gelada have bald, red patches on their chests which indicate health and reproductive status.

*Macaques* Macaques are the most widely disbursed and successful primate, other than humans, in the world. They range throughout Asia and are also found in North Africa and in Gibraltar. Macaques successfully live and thrive in varied habitats and climates ranging from Southern India to mountainous regions in Japan, with heavy

snowfall. Macaques are generally thought of as frugivores; however, depending upon seasonality and habitat, their diet can include a great deal of other foods including seeds, animal protein (invertebrates), bark, leaves, flowers, herbaceous growth, and roots. Many macaques are also heavily reliant on humans as a food source either through crop raiding or at temples or tourist spots, where they are provisioned.

## Apes

Apes show varying reliance on fruits, but all are considered somewhere on the spectrum of a frugivore-folivore or folivore-frugivore. Apes are the largest bodied and have the highest encephalization quotient (brain to body ratio) of all of the primates. While some apes (i.e., mountain gorillas) are more folivorous than frugivorous, the majority shows a preference for fruits, which are higher quality and have higher calorie content, supporting the energetic demands of a larger brain and body. Among the great apes, which includes chimpanzees (*Pan troglodytes* sp.), bonobos (*Pan paniscus*), orangutans (*Pongo abelii* and *Pongo pygmaeus*), gorillas (*Gorilla gorilla* sp. and *Gorilla beringei* sp.), and ancient and modern humans and their ancestors (*Australopithecus* sp. and *Homo* sp.), diets include, but are certainly not limited to, fruits, leaves, piths, and invertebrates. It has been shown that when given the opportunity, all great apes will preferentially eat fruits (Remis 2003).

### Asian Apes

*Gibbons and Siamangs* Gibbons and siamangs are the smallest bodied of the apes, which allow them to utilize more of the forest canopy than some of their conspecifics and are found only in Southeast Asia. Gibbons are highly frugivorous, relying most heavily on ripe fruits, though some species are more folivorous than others. Diet also consists of flowers, insects, and young leaves.

*Orangutans* Orangutans are a highly frugivorous species which impacts their overall social structure. Some of the preferred foods of orangutans

are durian fruit and figs. Additionally, tool usage has been observed in orangutans to obtain insects and saps from trees as well as hunting of other animals (i.e., slow loris) (van Schaik et al. 2003). As they are the largest-bodied arboreal animal, and trees fruit in patches, it's difficult for orangutans to live in social grouping. Females and their offspring will live together for up to 8 years, while dominant, or flanged, males will overlap in range with multiple females and their offspring.

Every few years, an ecological phenomena known as a masting or mast fruiting will occur, which produces an abundance of fruits on multiple trees of the same species simultaneously, allowing for large numbers of orangutans to congregate. Orangutans in the wild have been known to become obese during a mast fruiting. When mast fruiting occurs, orangutans will switch from their typical diet of leaves, bark, and some fruits to gorge themselves solely on high calorie fruits and fatty seeds until they are no longer available. It is not uncommon for orangutans, at the end of these periods of fruit abundance, to have enlarged fat deposits, which they rely on during the fruit scarcity that follows a mast fruiting.

### African Apes

*Gorillas* Habitat, elevation, and ecological niche greatly influences the diet of gorillas, the largest-bodied living (or extant) primate. Much of our knowledge of gorilla diet, ecology, and behavior come from the groundbreaking work on mountain gorillas (Fossey and Harcourt 1977; Schaller 1963). Because of these studies, all gorillas were long thought to be ground-dwelling leaf eaters. However, while mountain gorillas are specialized to higher altitudes and do forage mainly on the ground for leaves and herbaceous growth (Fossey and Harcourt 1977; Schaller 1963), western lowland gorillas are typically found in lower-altitude forests with a diet that varies seasonally (Yamagiwa and Basabose 2006). Moreover, western lowland gorillas are known to spend time in the trees, with females being able to move among the higher and smaller branches as they are smaller bodied and more agile than males. This increased access to multiple levels of the forest



allows for more food availability for females and juveniles.

Western lowland gorillas are now commonly classified as folivore-frugivores, as they prefer ripe fruit but will utilize leaves and herbs as staple foods and fallback foods (Remis 1997, 2003; Yamagiwa and Basabose 2006). Additionally, they will eat invertebrate animal prey (Tutin and Fernandez 1985) (typically by breaking open termite mounds), though it is not a significant source of their daily protein intake. High fruit consumption occurs during seasons when fruit availability is higher (Goldsmith 1999; Remis 1997), but they will switch to lower energy, fibrous herbs, leaves, and bark, when fruit availability is scarce (Dierenfeld 1997; Goldsmith 1999; Masi et al. 2009; Remis 1997; Rothman et al. 2008; Wobber et al. 2008).

Gorillas have an enlarged cecum and colon (portions of the large intestine) that is rich in species-specific gut microbiota, which facilitate the digestion of a high-fiber diet (up to 200 g/day). Wild gorilla diets are high in many vitamins and minerals, though sodium is often sought out in various ways depending on the species. Where mountain gorillas will eat decaying wood as a source of sodium, western lowland gorillas will travel to clearings in the forest called salines (along with other species, including forest elephants), to ingest mineral-rich soils.

*Chimpanzees and Bonobos* Chimpanzees in the wild eat a variety of foods including fruits, leaves, herbs, bark, and invertebrate and vertebrate animal protein (including eggs) (Wrangham 1977; Goodall 1986). Both chimpanzees and bonobos are highly frugivorous, and most of the protein content of their diets are plant based in the form of herbaceous leaves. In addition, chimpanzees are successful hunters and often cooperate together to obtain prey. A favorite food of chimpanzees, where available, are red colobus monkeys. Bonobos, on the other hand, rarely eat animal protein (though they will eat duiker sporadically) and eat a more frugivorous-folivorous diet. Chimpanzees and bonobos both regularly utilize tools to extract foods, most famously for termite fishing.

*Hominins: Humans and Their Ancestors* The similarities between the diets and dietary preferences among extant African apes and modern humans, prior to domestication, suggest that our last common ancestor likely shared a similar diet. For instance, gorillas, chimpanzees, and humans share similar gut morphology (Chivers and Hladik 1980), save the elongated large intestine of the gorilla. Moreover, apes and humans exhibit taste perception and food preferences that overlap (Dierenfeld 1997; Masi et al. 2009; Remis 1997; Rothman et al. 2008; Wobber et al. 2008). These similarities suggest that diets of very early hominins were likely more similar to those of extant (living) African apes than to contemporary human populations.

As hominins diverged from the common ancestor shared with gorillas and chimpanzees, there were shifts in diet, including the emergence of food preparation (Conklin-Brittain et al. 2002; Marshall and Wrangham 2007; Wobber et al. 2008; Wrangham 2009), food acquisition (and thus a greater variety in foods eaten), and eventually domestication. Changes in diet and the coinciding physical adaptations, including changes in cranial and dental morphology, are considered hallmarks in hominin evolution. As soft tissue cannot fossilize, it has been hard to understand the full morphological consequences of these dietary shifts to early hominin digestive anatomy and physiology over the course of evolution. However, while generalized gut morphology can be reconstructed from changes in torso shape in fossil species (Aiello and Wheeler 1995), gut morphology is plastic and is able to change in minor ways over short periods of time, depending on diet (Milton 1999).

The use of fire and subsequent heating and cooking of hominin foods alter the chemical structure and nutritional composition of consumed foods (Wrangham 2009). Moreover, a study has shown that even captive great apes, who have never eaten cooked food, when given the option, prefer it (Wobber et al. 2008). In addition, as hominins moved out of the forest and into the savanna, fallback foods likely shifted to underground storage organs (i.e., roots and tubers), which are lower in fiber content and more calorically dense than typical forest fallback foods such as mature leaves,

herbaceous leaves, bark, and pith (Conklin-Brittain et al. 2002). Moreover, fossil evidence suggests that during this time, hominins increasingly relied on wild game (Milton 1999).

While the advent of agriculture and crop domestication is relatively recent from an evolutionary perspective, humans have been domesticating and eating grains and other soft foods for thousands of years. Even with this prolonged exposure, humans physically appear to have been unable to keep pace with the myriad of dietary changes that have occurred with the advent of agriculture and the Industrial Revolution (Milton 1999).

## Cross-References

- ▶ [Cattarrhine Cognition](#)
- ▶ [Cattarrhine Communication](#)
- ▶ [Cattarrhine Life History](#)
- ▶ [Cattarrhine Morphology](#)
- ▶ [Cattarrhine Sensory Systems](#)
- ▶ [Hominoidea](#)
- ▶ [Insectivore Diet](#)
- ▶ [Primate Diet](#)

## References

- Aiello, L. C., & Wheeler, P. (1995). The expensive-tissue hypothesis: The brain and the digestive system in human and primate evolution. *Current Anthropology*, 36(2), 199–221.
- Chivers, D. J., & Hladik, C. M. (1980). Morphology of the gastrointestinal tract in primates: Comparisons with other mammals in relation to diet. *Journal of Morphology*, 16, 337–386.
- Conklin-Brittain, N. L., Wrangham, R. W., & Smith, C. C. (2002). A two-stage model of increased dietary quality in early hominid evolution: The role of fiber. In P. S. Ungar & M. F. Teaford (Eds.), *Human diet: Its origin and evolution*. Westport/London: Bergin and Garvey.
- Dierenfeld, E. S. (1997). Symposium on ‘nutrition of wild and captive wild animals’ plenary lecture. *Proceedings of the Nutrition Society*, 56, 989–999.
- Fashing, P. J. (2011). African colobine monkeys: Their behavior, ecology, and conservation. In C. J. Campbell, A. Fuentes, K. C. MacKinnon, S. K. Bearder, & R. M. Stumpf (Eds.), *Primates in perspective* (2nd ed., pp. 203–229). New York: Oxford University Press.
- Fossey, D., & Harcourt, A. H. (1977). Feeding ecology of free-ranging mountain gorilla (*Gorilla gorilla beringei*). In T. H. Clutton-Brock (Ed.), *Primate ecology* (pp. 415–447). London: Academic Press.
- Goldsmith, M. L. (1999). Ecological constraints on the foraging effort of western gorillas (*Gorilla gorilla gorilla*) at Bai Hokou, Central African Republic. *International Journal of Primatology*, 20, 1–23.
- Goodall, J. (1986). *The chimpanzees of Gombe. Patterns of behavior*. Cambridge, MA: Belnap Press.
- Kay, R. N. B., & Davies, A. G. (1994). Digestive physiology. In A. G. Davies & J. F. Oates (Eds.), *Colobine monkeys: Their ecology, behavior and evolution* (pp. 229–259). Cambridge: Cambridge University Press.
- Kirkpatrick, R. C. (2011). The Asian colobines: Diversity among leaf-eating monkeys. In C. J. Campbell, A. Fuentes, K. C. MacKinnon, S. K. Bearder, & R. M. Stumpf (Eds.), *Primates in perspective* (2nd ed., pp. 189–202). New York: Oxford University Press.
- Lambert, J. E., & Rothman, J. M. (2015). Fallback foods, optimal diets, and nutritional targets: Primate responses to varying food availability and quality. *Annual Review of Anthropology*, 44, 493–512.
- Marshall, A. J., & Wrangham, R. W. (2007). Evolutionary consequences of fallback foods. *International Journal of Primatology*, 28, 1219–1235.
- Masi, S., Cipolletta, C., & Robbins, M. M. (2009). Western lowland gorillas (*Gorilla gorilla gorilla*) change their activity patterns in response to frugivory. *American Journal of Primatology*, 71(2), 91–100.
- Milton, K. (1999). Nutritional characteristics of wild primate foods: Do the diets of our closest living relatives have lessons for us? *Nutrition*, 15(6), 488–498.
- Newton, P. N. (1992). Feeding and ranging patterns of forest Hanuman langurs (*Presbytis entellus*). *International Journal of Primatology*, 13, 245–285.
- Remis, M. J. (1997). Western lowland gorillas (*Gorilla gorilla gorilla*) as seasonal frugivores: Use of variable resources. *American Journal of Primatology*, 43, 87–109.
- Remis, M. J. (2003). Are gorillas vacuum cleaners of the forest floor? The roles of body size, habitat and food preferences on gorilla dietary flexibility and nutrition. In A. B. Taylor & M. L. Goldsmith (Eds.), *Gorilla biology: A multidisciplinary perspective* (pp. 395–404). Cambridge, MA: Cambridge University Press.
- Rothman, J. M., Dierenfeld, E. S., Hintz, H. F., & Pell, A. N. (2008). Nutritional quality of gorilla diets: Consequences of age, sex, and season. *Oecologia*, 155, 111–122.
- Schaller, G. B. (1963). *The mountain gorilla: Ecology and behavior*. Chicago: The University of Chicago Press.
- Tutin, C. E., & Fernandez, M. (1985). Foods consumed by sympatric populations of *Gorilla g. gorilla* and *Pan T. troglodytes* in Gabon: Some preliminary data. *International Journal of Primatology*, 6, 27–43.
- van Schaik, C. P., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, C. D., Singleton, I., Suzuki, A., Utami, S. S., &

- Merrill, M. (2003). Orangutan cultures and the evolution of material culture. *Science*, 299, 102–105.
- Wobber, V., Hare, B., & Wrangham, R. (2008). Great apes prefer cooked food. *Journal of Human Evolution*, 55, 340–348.
- Wrangham, R. W. (1977). Feeding behavior of chimpanzees in the Gombe National Park, Tanzania. In T. H. Clutton-Brock (Ed.), *Primate ecology: Studies of feeding and ranging behavior in lemurs, monkeys and apes* (pp. 503–538). London: Academic Press.
- Wrangham, R. (2009). *Catching fire: How cooking made us human*. New York: Basic Books.
- Yamagiwa, J., & Basabose, A. K. (2006). Diet and seasonal changes in sympatric gorillas and chimpanzees at Kahuzi-Biega National Park. *Primates*, 47(1), 74–90.

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## Sneaky Copulator

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### Synonyms

[Covert copulator](#); [Extra-pair copulation](#); [Sneak copulator](#); [Sneaker males](#); [Sneakers](#); [Sneaky mating](#)

### Definition

An individual performing copulatory behavior while withholding information about the sexual event (e.g., visual or auditory) for bystanders that could possibly prevent or disrupt the copulation.

### Introduction

From an evolutionary viewpoint reproduction is one of the most important goals of every living being. Evolutionary theory predicts that all organisms strive to have as much surviving offspring as possible. Therefore, animals have developed behaviors that increase their chances of reproduction. Because the number of available mating partners is not infinite, sexual competition is highly prevalent in animals. Animals have developed strategies to increase their chances in the

competition for mating opportunities. Although many different mating systems exist across animal species, strategies for increasing mating opportunities are often similar across mating systems. There are often individual differences in strength and power between males or females. A widespread behavior that is often used by strong or powerful individuals is to monopolize copulations. Monopolization may be achieved by behaviors such as mate guarding defending a territory with copulation partners or punishing others that (attempt to) copulate. An alternative strategy, which is more often used by less strong or less powerful individuals, is sneaky copulation; by concealing sexual behavior, sneak copulators evade mate guarding and/or punishment.

### Monopolization, Mate Guarding, and Punishment

Monopolization occurs when one individual is in a position that allows it to restrict the number of copulations performed by competitors. This position may be a dominant individual which has a generally acknowledged hierarchical position which enforces others to restrict copulatory behavior in its presence (Overduin-de Vries et al. 2013). In these hierarchical systems, there is an alpha individual, usually a male (but there are also harem mating systems with an alpha female leader), which has a lot of power because he/she has proven to be the strongest, or he/she is born in

the right family. Monopolization may be achieved by the mere presence of a socially dominant or physically stronger individual. This occurs when lower-ranking or physically weaker individuals abrupt their mating attempts upon confrontation with a possible monopolizer, in order to prevent harmful conflicts. A generally used tactic by monopolizers is mate guarding; following and defending (a) particular (fertile) opposite sex individual (s). In socially monogamous species individuals follow their partner around and prevent it from copulating with others. Likewise dominant individuals in social groups mate guard fertile individuals. Mate guarding is most effective in species where the fertile phase is detectable for the opposite sex, because this limits the time frame in which mate guarding is necessary. Besides, in social groups ovulation synchrony impedes monopolization since monopolizers cannot mate guard all fertile individuals simultaneously. Another monopolizing tactic is to use aggression in order to force others to give up their copulation attempt (e.g., Gouzoules 1974). For example, monkey females that attempt to copulate with males other than the alpha male face punishment in the form of being chased, being threatened, or receiving physical aggression. Both the female and the male sneaky copulator risk punishment in monkeys. After disruption, the alpha male often copulates with the interrupted female.

### **Mating Systems Including Sneaky Copulators**

Sneak copulation occurs in mating systems where individuals are restricted in choosing their mating partners, e.g., in systems where monopolization or mate guarding occurs or where sexual behavior is punished by certain individuals. These are systems with pair bonds, systems where mating occurs within fixed groups and harem groups.

Monogamous pair bonding is common across the animal kingdom, especially among birds (93% of species) (Lack 1968) and primates (12% is monogamous) (Rutberg 1983). However after close inspection of sneaky behavior and DNA

comparisons of parent offspring combinations, it becomes clear that much less species are also sexually monogamous (Griffith et al. 2002). Extra-pair copulations are often the result of sneak copulators that conceals its copulations for its partner. Examples of species that are known for their strict social monogamy but that are nonetheless sneak copulators are Lar Gibbons (*Hylobates lar*) (Reichard 1995), zebra finches (*Taeniopygia guttata*) (Houtman 1992), and beavers (*Castor canadensis*) (Crawford et al. 2008).

Sneaky copulation also occurs in animal species where mating is restricted within small groups. For example, dunnocks live in monogamous couples or in small groups where two or three males cooperatively defend a territory with one or multiple females. The most dominant male intensively guards the female(s) throughout the mating season, but especially when food is scattered and the female home range expands, monopolization is difficult (Davies and Hartley 1996). The subordinate male(s) almost always fertilize some of the eggs. This is not only the result of the pursue of the subordinate males but also of the female, which actively attempts to sneak away from the dominant male to have mating opportunities with the subordinate males.

Many species such as elephant seals (de Bruyn et al. 2011), bighorn sheep (Hogg 1987), and long-tailed macaques (Overduin-de Vries et al. 2013) live in harem groups. The power of the group leader gives him/her exclusive right to copulate with the opposite sex group members. For example, elephant seal males risk their live in injurious fights with sharply teathed opponents. The winner of these fights will become the leader of dozens or even hundreds of females. However, an alternative mating tactic exists that creates opportunities for siring offspring for individuals that prefer to stay clear of risky competition: sneak copulation at sea (de Bruyn et al. 2011). This sneak copulator tactic may be particularly worthwhile for individuals that are less likely to win male-male fights. Similarly, bighorn sheep live in harem groups where one alpha male monopolizes the majority of fertile females, by mate guarding (Hogg 1987). However, females occasionally run away from their monopolizer and sneak



copulators profit by courting them and copulating quickly away from the group leader (Hogg 1987).

frequency of males and females and their strategies (Gross 1996).

## Conflict between and within the Sexes

The existence of sneak copulation within a species is often the result of a conflict between or within the sexes. Sneak copulation can be a strategy that has evolved as a female strategy within the framework of the conflict between the sexes (Parker 2006) but also as a male strategy to outcompete other males. There are different things at stake for males and females in a mating market. When producing offspring, females generally invest more than males in terms of larger gametes and the extra burden of gravidity (Clutton-Brock 1991). Therefore, females generally prefer polygamous mating which allows them to select the better sperm for their costly egg. Exceptions to this preference are often related to paternal care. If paternal care significantly contributes to the survival of offspring, females may benefit more from a single copulation partner that cares for their offspring (Gubernick and Teferi 2000), than from multiple partners that are not taking care of the offspring. However, the most successful strategy for females would be to profit from a male's paternal investment while sneakily copulating with other males in order to improve the genetic quality of their offspring (Kempnaers et al. 1992).

Males, on the other hand, have developed strategies to prevent parental investment in offspring that is sired by their neighbors. For example, monopolization of females is a strategy that limits paternity uncertainty. However, some males are better in monopolizing females than others. Whereas strong and/or powerful males profit most from monopolizing females, weaker and/or less powerful males are less likely to win contests over females and have a higher risk of injury during these contests. Therefore, alternative reproductive strategies exist for males (Gross 1996) such as sneak copulation. The relative success of both strategies, monopolizing or sneaking, depends on the status of the male and the

## Withholding Information

Sneak copulators conceal their copulations by withholding information from possible eavesdroppers, which could possibly disrupt or prevent their copulation. They withhold either visual or auditory information or both. For example, long-tailed macaques prefer to copulate near opaque structures blocking the view of a possible audience. Likewise, they copulate more often when the group leader is in a visually separated enclosure (Overduin-de Vries et al. 2013). This way they prevent possible competitors from seeing the copulation, minimizing the possibility of being disrupted during copulation.

Another way of concealing copulation is by suppressing copulation calls (Townsend et al. 2008, Clay and Zuberbuhler 2011). Low-ranking female chimpanzees (*Pan troglodytes schweinfurthii*) suppress copulation calls when high-ranking females are present. This way, low-ranking females avoid female-female competition, which can be severe in this species.

Another form of sneak copulation for males is mimicking a female. These fake females can sneak within the territory of another male or approach another male's partner without being attacked by him and perform sneaky copulation. When employing the mimic tactic, males conceal their true color during the approach of the female, withholding information about their identity, being a male.

## Cognitive Level

Withholding information from another individual is sometimes interpreted as higher-order cognition under the term deception, but it does not need to be. By using simple rules of thumb, such as "freeze behavior or change color when in close proximity of a strong or dominant individual," animals can conceal behavior (Amici et al. 2009) without making inferences about what another

individual can see or hear. These rules of thumb can be learned by simple operant learning when sexual behavior in close proximity of dominant individuals is linked with punishment. Therefore, animals with cognitive capacities that are at least capable of learning by operant conditioning are equally likely to be sneak copulators as are more intelligent species. Moreover, mimicry is possible without operant conditioning. In some species the female mimics are inflexible traits that are genetically based (Sinervo and Lively 1996) or fixed during early development (Emlen 1997). Therefore, this tactic can be used by animals that are less cognitively advanced including fish (Dominey 1980), reptiles (Sinervo and Lively 1996), and isopods (Shuster and Wade 1991). In contrast, other mimicking species, such as the giant cuttlefish, can flexibly adjust their appearance and resemble a female when they are sneakily copulating, while they return back to male coloration afterwards (Norman et al. 1999). This flexible use of color mimicry does require cognitive processes such as operant conditioning.

## Sneaky Copulators and Human Sexual Behavior

Within human behavior, there is enough evidence that sneak copulation is a substantial contributor to the fitness of an individual. For example, women copulate more often sneakily with a lover around the time of ovulation (Gildersleeve et al. 2014). This indicates that sneak copulation is an important strategy for women to fertilize their egg with sperm other than their partners'. The rationale behind this strategy is that women try to get the best of two worlds without being aware of using this strategy. They choose a long-term partner that is caring, protecting, and a good father, while they choose strong, intelligent, high status, and good-looking lovers to fertilize their egg. There is also evidence that males have evolved counterstrategies as a response to female promiscuity (Shackelford et al. 2005). For example, the longer a man has been away from his wife, the larger will be his ejaculate. This larger amount of sperm will give him an advance in case his

sperm has to compete with sperm from another man. Moreover, there are indications that human sperm cells can selectively kill the sperm cells of rivals within the female reproductive tract (Baker and Bellis 1988). Although this theory is debated by many researchers, and convincing empirical evidence is difficult to collect, it is not the first case where sperm cells use complicated strategies to combat rival sperm (Percy et al. 2014).

## Cross-References

- ▶ [Assortative Mating](#)
- ▶ [Cheating](#)
- ▶ [Competition](#)
- ▶ [Covert Copulation](#)
- ▶ [Deception](#)
- ▶ [Extra-Pair Copulation](#)
- ▶ [Mate Guarding](#)
- ▶ [Mating](#)
- ▶ [Primate Mating Systems](#)
- ▶ [Sperm Competition](#)
- ▶ [Tactical Deception](#)

## References

- Amici, F., Call, J., & Aureli, F. (2009). Variation in withholding of information in three monkey species. *Proceedings of the Royal Society B-Biological Sciences*, 276, 3311–3318.
- Baker, R. R., & Bellis, M. A. (1988). Kamikaze sperm in mammals. *Animal Behaviour*, 36, 936–939.
- Clay, Z., & Zuberbuhler, K. (2011). The structure of bonobo copulation calls during reproductive and non-reproductive sex. *Ethology*, 117, 1158–1169.
- Clutton-Brock, T. H. (1991). *The evolution of parental care*. Princeton. New Jersey: Princeton University Press.
- Crawford, J. C., Liu, Z. W., Nelson, T. A., Nielsen, C. K., & Bloonquist, C. K. (2008). Microsatellite analysis of mating and kinship in beavers (*Castor canadensis*). *Journal of Mammalogy*, 89, 575–581.
- Davies, N. B., & Hartley, I. R. (1996). Food patchiness, territory overlap and social systems: An experiment with dunnocks *Prunella modularis*. *Journal of Animal Ecology*, 65, 837–846.
- de Bruyn, P. J. N., Tosh, C. A., Bester, M. N., Cameron, E. Z., McIntyre, T., & Wilkinson, I. S. (2011). Sex at sea: Alternative mating system in an extremely polygynous mammal. *Animal Behaviour*, 82, 445–451.

- Dominey, W. J. (1980). Female mimicry in male bluegill sunfish – a genetic-polymorphism. *Nature*, *284*, 546–548.
- Emlen, D. J. (1997). Alternative reproductive tactics and male-dimorphism in the horned beetle *Onthophagus Acuminatus* (Coleoptera:Scarabaeidae). *Behavioral Ecology and Sociobiology*, *41*, 335–341.
- Gildersleeve, K., Haselton, M. G., & Fales, M. R. (2014). Do Women's mate preferences change across the ovulatory cycle? A meta-analytic review. *Psychological Bulletin*, *140*, 1205–1259.
- Gouzoules, H. (1974). Harassment of sexual-behavior in stump-tail macaque, *macaca-arctoidesi*. *Folia Primatologica*, *22*, 208–217.
- Griffith, S. C., Owens, J. P. F. & Thuman, K. A. (2002). Extra pair paternity in birds: a review of interspecific variation and adaptive function. *Molecular ecology*, *11*, 2195–2212.
- Gross, M. R. (1996). Alternative reproductive strategies and tactics: Diversity within sexes. *Trends in Ecology & Evolution*, *11*, 92–98.
- Gubernick, D. J., & Teferi, T. (2000). Adaptive significance of male parental care in a monogamous mammal. *Proceedings of the Royal Society B-Biological Sciences*, *267*, 147–150.
- Hogg, J. T. (1987). Intrasexual competition and mate choice in rocky mountain bighorn sheep. *Ethology*, *75*, 119–144.
- Houtman, A. M. (1992). Female zebra finches choose extra-pair copulations with genetically attractive males. *Proceedings of the Royal Society B-Biological Sciences*, *249*, 3–6.
- Kempenaers, B., Verheyen, G. R., Vandenbroeck, M., Burke, T., Van Broeckhoven, C., & Dhondt, A. A. (1992). Extra -pair paternity results from female preference for high-quality males in the blue tit. *Nature*, *357*, 494–496.
- Norman, M. D., Finn, J., & Tregenza, T. (1999). Female impersonation as an alternative reproductive strategy in giant cuttlefish. *Proceedings of the Royal Society B-Biological Sciences*, *266*, 1347–1349.
- Overduin-de Vries, A. M., Olesen, C. U., de Vries, H., Spruijt, B. M., & Sterck, E. H. M. (2013). Sneak copulations in long-tailed macaques (*Macaca fascicularis*): no evidence for tactical deception. *Behavioral Ecology and Sociobiology*, *67*, 101–111.
- Parker, G. A. (2006). Sexual conflict over mating and fertilization: An overview. *Philosophical Transactions of the Royal Society B-Biological Sciences*, *361*, 235–259.
- Pearcy, M., Delescaille, N., Lybaert, P., & Aron, S. (2014). Team swimming in ant spermatozoa. *Biology Letters*. doi:10.1098/rsbl.2014.0308.
- Reichard, U. (1995). Extra-pair copulations in a monogamous gibbon (*hylobates lar*). *Ethology*, *100*, 99–112.
- Rutberg, A. T. (1983). The evolution of monogamy in primates. *Journal of Theoretical Biology*, *104*, 93–112.
- Shackelford, T. K., Pound, N., & Goetz, A. T. (2005). Psychological and physiological adaptations to sperm competition in humans. *Review of General Psychology*, *9*, 228–248.
- Shuster, S. M., & Wade, M. J. (1991). Equal mating success among male reproductive strategies in a marine isopod. *Nature*, *350*(6319), 608–610.
- Sinervo, B., & Lively, C. M. (1996). The rock-paper-scissors game and the evolution of alternative male strategies. *Nature*, *380*(6571), 240–243. doi:10.1038/380240a0.
- Townsend, S. W., Deschner, T., & Zuberbühler, K. (2008). Female chimpanzees use copulation calls flexibly to prevent social competition. *PloS One*, *3*, e2431.
- Lack, D. (1968). *Ecological Adaptations for Breeding in Birds*. London: Methuen Ltd.

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## Robert Mearns Yerkes

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Robert Mearns Yerkes (May 26, 1876 – February 3, 1956) was an American comparative psychologist best known for initiating the intelligence testing movement and establishing the first American primate laboratory. His namesake, the Yerkes National Primate Research Center, is now located at Emory University in Atlanta, Georgia. The Yerkes-Dodson Law that describes the parabola-shaped relationship between performance and arousal is well known and used in a multitude of disciplines (Hilgard 1965).

Growing up on a rural farm in Bucks County, Pennsylvania, Robert M. Yerkes, in his 1930 autobiography, recalled a happy childhood that inspired curiosity and allowed for a young scientist's mind to flourish. In his early years, however, Robert and his eldest sister both contracted scarlet fever. She passed away but Robert survived (Yerkes 1930) although he was plagued with chronic fatigue for many years following (Hilgard 1965). He had three other siblings, all quite a bit younger than Robert. Although Robert Yerkes' mother and father never attended college, he had an uncle and cousin who practiced medicine. They encouraged the young Yerkes to study medicine in order to

attain an education that would provide an easier lifestyle, a doctor's lifestyle, rather than the difficult and labor-intensive livelihood of his father, a farmer (Yerkes 1930).

At the age of sixteen, Yerkes' uncle, Dr. Edward Atkinson Krusen, provided him room and board along with a small compensation for schooling at Ursinus College in exchange for household chores. Five years later, in 1892, he graduated with an Atrium Baccalaurea (A.B.) degree, or more commonly known as a Bachelor of Arts. Yerkes was then offered a one-thousand-dollar loan from Harvard University to pursue graduate work in zoology. Needing the money, Yerkes abandoned medicine and began as a provisional undergraduate for 1 year beginning in 1897. Yerkes proved worthy of graduate status and gained another A.B. degree along the way. His first paper, *Reaction of Entomostraca to Stimulation by Light* (Yerkes 1899), was published under the supervision of Charles B. Davenport in the Laboratory of Comparative Zoology in 1899 at Harvard University (Yerkes 1930).

It was Josiah Royce, an American philosopher, who suggested comparative psychology to Yerkes that began his study of animal behavior and cognition and how it relates to that of different animals or humans, thus pairing his main interests, zoology and psychology. Hugo Münsterberg, shortly thereafter, extended a position to Yerkes in his laboratory to study comparative psychology and subsequently became a mentor and dear friend. Over the course of his graduate career,

Yerkes lectured in courses on genetic and comparative psychology as well as conducted what he referred to as psychobiological research. His dissertation, *The Psychic Process of the Frog* that examined learning in the frog while in a labyrinth, was completed in 1902 for which he earned a Doctorate of Philosophy in Psychology from Harvard University (Yerkes 1930).

Yerkes' research interests first included various aspects of organic receptivity and its relation to behavior. Using subjects such as amphibians and reptiles, he frequently published on these topics between 1905 and 1912 (Dewsbury 1996). He was also dedicated to the advancement of comparative psychobiological methods and, therefore, devoted much of his research and time to the development of tasks that could reliably measure phenomenon across different species (Yerkes 1930). Soon his subject choice evolved from amphibians and reptiles to lower mammals. *The Dancing Mouse* (1907), his first book, helped establish the use of mice and rats as standard laboratory subjects in psychological testing (Dewsbury 1996). His goal ultimately became to establish a comparative psychobiological research center that would house anthropoid subjects (Yerkes 1930).

After graduation, Yerkes attained a position at Harvard and remained there for the next 15 years (1902–1917). As an instructor and later as assistant professor of comparative psychology, his colleagues included eminent scholars such as William James, Hugo Münsterberg, Francis Peabody, George Santayana, Dickinson Miller, Robert MacDougall, Edwin B. Holt, Ralph B. Perry, and John D. Dodson (Yerkes 1930). In 1908, Yerkes and Dodson formulated the famous Yerkes-Dodson Law describing the parabola-shaped relationship between arousal and performance (Dewsbury 1996).

With Yerkes marriage to biologist Ada Watterson in 1909, his home and professional life flourished as she participated with him in numerous research projects and cowrote one of his classics (Yerkes 1930), *The Great Apes: A Study of Anthropoid Life* (Yerkes and Yerkes 1929).

Although Yerkes studied observable phenomenon, he believed psychologists should also study

mental processes (Hilgard 1965). He thought it was possible to empirically investigate the phenomena of experience in relation to the environment in which it occurred. Therefore, he rejected John B. Watson's radical behaviorism, but as a participant in the developmental phase of the theory with Watson, he found merit in parts of behavior theories (Yerkes 1930). Records of correspondence between the two provide evidence of close collaboration and sharing of ideas (Hilgard 1965). Watson and Yerkes, through their collaborations, also contributed to the improvement and standardization of methods for the comparative study of vision (Yerkes 1930).

Edward B. Titchener, a British psychologist who worked with Wilhelm Wundt, often exchanged letters with Yerkes in which they discussed the psychology of the self. Yerkes was intrigued with the use and measurement of introspection and wrote his first and only textbook, *An Introduction to Psychology* (1911), to explore the topic thoroughly and gain a clearer conceptual understanding of introspection and the psychology of the self (Yerkes 1930). Furthermore, Yerkes was responsible for the first American scientific journal devoted to the study of animal behavior in 1911, the *Journal of Animal Behavior* (Burkhardt 1987).

Beginning in 1913, Yerkes became a hospital psychologist at Boston Psychopathic Hospital while continuing his Harvard obligations. During the next 5 years at the hospital, he discovered a need for improved techniques and measurement regarding psychobiological issues. In 1915, Yerkes helped to create the Yerkes-Bridges Point Scale of Intelligence which measured aspects of intellectual activity and the multiple-choice method for the study of ideational behavior (Yerkes 1930).

In 1917, The University of Minnesota asked Yerkes to reorganize the psychology department and establish a new laboratory. After much consideration, Yerkes reluctantly accepted the position and left Harvard and the Boston Psychopathic Hospital in the spring of 1917 for Minnesota. Yerkes did manage to set the proper motions in place for the psychology department and secure a location for a new laboratory, but his stay at

Minnesota was cut short with America's entry into the First World War (Yerkes 1930).

One year prior, in 1916, Yerkes had become president of the American Psychological Association (APA), Psychology's flagship organization. As such, he found himself at the forefront of Psychology when America entered World War I in April of 1917. A group of psychologists, including Yerkes, happened to be at Harvard the time. They felt compelled to aid in the war efforts and recognized an application of Psychology was needed (Yerkes 1930). Thus, the intelligence testing movement began, and the Army Alpha and Beta tests were born out of the Committee on the Psychological Examination of Recruits that Yerkes chaired. The Army Alpha test allowed matching of recruits to skills required by appropriate positions in the army. The Beta test served the same function but was administered to foreigners and those who were illiterate. As president of APA, Yerkes' role was to take the initiative in organizing the testing effort. He established the appropriate relations with the Medical Department of the Army despite several obstacles and, through this arm of service, became personally responsible for the psychological examination of recruits. For the first time, intelligence tests were administered to a group of people instead of individually allowing 1,726,000 United States soldiers to be tested during the movement (Hilgard 1965).

Psychology received positive public acknowledgment for the success of the intelligence testing movement allowing Yerkes and other psychologists to begin testing the general population with ease. The tests used have been called the forerunners of standardized tests such as the scholastic aptitude test (SAT), which measures college readiness. Yerkes also published two books that continue to serve as models for the advancement of intelligence testing, *Army Mental Tests* (1920) and *Psychological Examining in the US Army* (1921) (Hilgard 1965).

The intelligence-testing movement also demonstrated Psychology's usefulness as a profession. Given Yerkes' vital role, he is often credited for aiding in the application of psychology in a professional capacity (Hilgard 1965). This is

important because the role of American psychologists at the time was to conduct research exclusively.

Psychology accumulated massive accumulation of data after the completion of the first mass-scale-testing movement. Yerkes's personal analyses led him to controversial conclusions about the origins of racial and ethnic differences in intelligence that coincided with the eugenics movement in the US and abroad. Along with racial and ethnic differences, he also found generational differences in IQ which led him to conclude that IQ was declining in the US. His interpretation of the findings about race and ethnicity resulted in more restrictive immigration laws. Eventually, his conclusions were refuted, but the data remain a psychometrist's treasure trove (Hilgard 1965).

Shortly after the 1918 Armistice, Yerkes had to choose between continuing his work with mental testing to aid the war efforts or following his academic pursuits and returning to the position at the University of Minnesota that was interrupted by the war. He ultimately decided to abandon his post at Minnesota to complete a large report of Psychology's effort during the war and to begin securing financial support for the systematic study of anthropoid apes (Yerkes 1930).

Yerkes joined the faculty at Yale University in 1924 where he remained for the next 20 years. He began pursuing his initial goals of opening a primate facility and renewed his investigations of the great apes. He soon was the top researcher in the field. Previously, he had published a plan of action to open a primate facility (Yerkes 1916), but the proposal lacked financial support. His professorship at Yale provided him with the time necessary to acquire the finances and complete his plan. In the summer of 1924, he traveled to Havana, Cuba to observe a large colony of primates (Yerkes 1930). Upon returning, he moved to New Haven, Florida and purchased two chimpanzees, Chim and Panzee, from a zoo. He brought the two chimps home, where they lived in a bedroom and were taught to behave much like small, human children. Yerkes documented this experience in his paper *Almost Human* (Yerkes 1925; Hilgard 1965).



In 1929, he reached his long-time goal and established the Yale Laboratories of Primate Biology in Orange Park, Florida. It was the first center for the study of the neural and physiological bases of behavior and the first primate laboratory of comparative psychology (Yerkes 1930). After Yerkes resignation as director in 1941, the center was renamed Yerkes Laboratories of Primate Biology. Ninety chimpanzees were studied under his direction. Yerkes' publication, *Chimpanzees: A Laboratory Colony* (1943), established the significance of studying primate behavior to gain understanding about human behavior and was his last work. Yerkes retired from Yale University in 1944 (Hilgard 1965).

After retirement, Yerkes continued to serve as chairman of the National Research Council Committee for Research on Problems of Sex (1921–1947). During this time, he was fundamental in the sponsorship of projects that led to such studies as the Kinsey report which focused on human sexual behavior (Hilgard 1965).

On February 3, 1956, at age 79, Yerkes passed away in New Haven, Connecticut, from coronary thrombosis after spending 2 years as an invalid (Hilgard 1965). Near Yale University, he is buried in Evergreen Cemetery in New Haven, Connecticut, with his wife who died in 1965. After his death, the Yerkes National Primate Research Center was relocated to Atlanta, Georgia, at Emory University where anthropoid subjects are still studied today (Hilgard 1965).

## Cross-References

- ▶ [Comparative Psychology](#)
- ▶ [Emory](#)

- ▶ [IQ](#)
- ▶ [Primate Research Centers](#)
- ▶ [Yerkes Primate Research Center](#)

## References

- Burkhardt, R. W. (1987). The Journal of animal behavior and the early history of animal behavior studies in America. *Journal of Comparative Psychology*, 101(3), 223.
- Dewsbury, D. A. (1996). Robert M. Yerkes: A psychobiologist with a plan. In G. A. Kimble, C. A. Boneau, & M. Wetheimer (Eds.), *Portrait of pioneers in psychology* (Vol. 2, pp. 87–104). Washington, DC: Psychology Press.
- Hilgard, E. R. (1965). Robert Means Yerkes: May 26, 1876 – February 3, 1956. *Biographical Memoirs of the National Academy of Sciences of the United States of America*, 38, 385–425.
- Yerkes, R. M. (1899). Reaction of Entomostraca to stimulation by light. *American Journal of Physiology – Legacy Content*, 3(4), 157–182.
- Yerkes, R. M. (1907). *The dancing mouse: A study in animal behavior*. New York: Macmillan.
- Yerkes, R. M. (1911). *Introduction to psychology*. New York: Holt.
- Yerkes, R. M. (1916). Provision for the study of monkeys and apes. *Science*, 43, 231–234.
- Yerkes, R. M. (1921). In R. M. Yerkes (Ed.), *Psychological examining in the United States Army*, (Vol. 15). Washington: US Government Printing Office.
- Yerkes, R. M. (1925). *Almost human*. New York: Century.
- Yerkes, R. M. (1930). Robert Mearns Yerkes: Psychobiologist. In C. Murchison (Ed.), *A history of psychology is autobiography* (Vol. 2, pp. 381–407). Worcester: Clark University Press.
- Yerkes, R. M. (1943). *Chimpanzees: A laboratory colony*. New Haven: Yale University Press.
- Yerkes, R. M., & Yerkes, A. W. (1929). *The great apes: A study of anthropoid life*. New Haven: Yale University Press.
- Yoakum, C. S., & Yerkes, R. M. (1920). *Army mental tests*. New York: Henry Holt and Company.

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## Turing Test

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### Synonyms

[Discourse](#); [Imitation game](#); [Hidden humans](#); [Lying](#); [Machine thinking](#); [Misidentification](#)

### Introduction

The ability of humans, and indeed other animals, to think plays a critical role in their cognition, understanding, and communication. But what exactly does it mean for an entity to think? Is it possible to measure thinking in some way? Can a machine be made to think in the same sort of way as a human?

Turing's imitation game, commonly known as the Turing test, was originally posed by Alan Turing as a "closely related" alternative to the question of whether or not a machine could be said to think (Turing 1950), something which could be "expressed in relatively unambiguous words." With regard to the question "Can machines think?" Turing actually felt this "to be too meaningless to deserve discussion." An important reason for this was the problem of agreeing on "definitions of the meaning of the terms 'machine' and 'think'." With regard to

machines, Turing did though exclude biological systems such as cellular growths (Warwick et al. 2010) and even "men born in the usual manner," stating "we only permit digital computers."

Since that paper appeared, a lot of discussion has focused on the concept of machine thinking and whether it can be humanlike at times or even whether it will ever be possible to copy human thinking in all its aspects (Dennett 1998; Dreyfus and Dreyfus 2009; Minsky 1982; Shah 2010). Turing suggested, "May not machines carry out something which ought to be described as thinking but which is very different from what a man does?" (Turing 1950). As a result, some researchers in the field regard the test as laying the foundations for what is now known as artificial intelligence (AI), even considering it to be AI's "empirical goal" (Harnad 1992).

The game involves human interrogators attempting to ascertain the nature of hidden (human and computer) entities with whom/which they are communicating. As indicated by Turing in Turing (1950), each discourse lasts for a period of 5 minutes only, and at the end of that time, the interrogator is charged with making the "right identification" by clearly identifying the nature of their hidden discourse partners by declaring which is the human and which is the machine (Warwick and Shah 2016a).

In considering the game in further depth, one is faced with numerous intriguing questions regarding human and machine communication and behavior. When comparing a human's ability to

communicate, one immediately has to consider the fallibility, biases, and preconceptions of that person. One also must take into account important aspects of human nature such as lying, misunderstanding, lack of knowledge and humor, and never mind stupidity.

Over the last few years, a number of practical Turing test sessions have been organized involving some of the best conversation machines in the world; these followed as closely as possible with the test description as given by Turing himself in his seminal paper of 1950 (Turing 1950). One set of such experiments was held at Bletchley Park, England, in 2012. Another was held at the Royal Society, London, in 2014. The latter involved the largest number of tests ever staged in any single event.

In this article, the author reports on actual transcripts from these tests as a basis to investigate just what it takes to fool a human interrogator and how examples of the use of humor and lying have affected decisions. In addition, a look is taken at a series of cases in which human communicators have been clearly categorized by interrogators as definitely being machines and others in which machine communicators have been clearly categorized by interrogators as being human.

The transcripts between judges and hidden entities presented here are taken from tests in which a human judge carried out a 5-minute-long conversation with two hidden entities in parallel. One of the entities was a human and the other was a machine. It was very much up to the judge as to the nature of the conversation, and it was their decision as to how much time they spent conversing with each of the entities during the 5-minute period.

In a particular session, a judge conducted five separate tests. In their first test, they witnessed a hidden human pitted against a hidden machine. Of course the judge would not know which was which; they would simply be aware of two hidden entities and have to make their own decision on the nature of the entities, although they had been informed a priori that one entity was human and one was a machine. The second test conducted by the judge then involved a different human pitted against a different machine, although again they

would not be aware of each entity's nature. And so it would go on until the judge had conducted all their five tests in that session. At the end of each test, they were asked to state for each entity if they thought that it was a human or a machine or if they were unsure.

In the tests, the hidden humans were asked merely to be themselves, although they were requested not to give away their specific identity or personal information. They were not given any incentive to behave in a particular way and were given no payment at all. Of course this did not prevent any human from giving false information, which is something that humans do frequently. The tests were "unrestricted conversations," which meant the judge could ask anything or introduce any topic within the boundaries of courtesy (the judges had been informed however that there may be children among the hidden human entities).

## Turing Test Details

The conversations presented here were realized as a result of five-minute-long tests of human judge-hidden entity interaction, to conform to Turing's original wording in computing machinery and intelligence (Turing 1950).

What this paper does is to present a number of transcripts taken from practical Turing tests, which were held under strict conditions with many external viewers first at Bletchley Park, England, on June 23, 2012. The date marked the 100th anniversary of Turing's birth and the venue was that at which, during the Second World War, Turing led a team of code breakers to crack the German Enigma machine cipher. The second set of tests was held on June 6–7, 2014 at the Royal Society, London, of which Alan Turing was a fellow. Five different machines took part in both sets of tests along with 30 different judges and 30 hidden humans against which the machines were compared in terms of their conversational ability. Although the machines were common to the two experiments, the judges and hidden humans were a different collection of people.

In this article, one is certainly interested in how good or bad the machines are; indeed, it is interesting to look at how good they can be. But one is also interested in the operational performance of the judges and specifically how they interacted in conversation with hidden entities. Hidden humans are, by definition, human, but (Shah and Warwick 2010; Warwick and Shah 2015a) can themselves be misidentified on occasion? An attribution of *humanness* by a human interrogator to a hidden interlocutor in a practical Turing test is dependent on the judge's own values of what constitutes humanlike conversational behavior. Good performance of machines is largely discussed elsewhere (Warwick and Shah 2014a), although a couple of examples are given here in a separate section for comparative purposes.

A look is taken into Turing's statement that the test/game can be considered as a replacement for the question "Can machines think?" (Turing 1950). While it is acknowledged that the results in each case depend on the performance of the judge, far from the conditions of the game saying nothing about the judge, this aspect is seen here to be very much a critical part of the test itself. Importantly, in the test, machines are pitched against (hidden) humans under the critical analysis of other (interrogator) humans. These are all very important aspects of what the test is about and are certainly not points of fallibility of the game as has been suggested by Hayes and Ford (1995).

In the sections that follow, different examples of practical tests are given, and an attempt is made to cover a wide range of problem areas as they exist at present, which the test highlights. In each case, discussion on the transcript is carried out within that section, where it is pertinent. However, a number of universal comments are also made in the conclusions section toward the end of the article.

The transcripts considered in this paper appear exactly as they occurred. They have not been altered in any way in terms of the sequence or wording or corrected spelling. Once an utterance was outputted, it was not possible for the judge or hidden entity to alter it in any way. The timings shown are accurate, actual timings on the days

(UK time) involved. Any spelling mistakes or other grammatical errors were exactly as they happened. They are not due to editorial errors. In the transcripts, the interviewer/judge is always denoted as "judge," whereas the hidden interlocutors, machine or human, are denoted as "entity."

## Lying

Lying is a part of human nature and therefore has a role to play when it comes to the Turing test. The machine's goal is deception attempting to mislead the interrogator that it is a human. Meanwhile, hidden humans are requested not to give away exactly who they are through revealing personal details, as this might aid the interrogator, but apart from that they can simply be themselves. Lying can take on many different forms from a white lie to an unintentional lie to a complete untruth. What one is interested in is the effect of a lie on the decision taken by the interrogator. Please see Warwick and Shah (2016b) for an in-depth analysis of these and many more transcripts.

Transcript 1:

[12:43:23] Judge: Why hello there!

[12:43:41] Entity: Why hello to you too!

[12:44:51] Judge: How are you feeling on this fine day?

[12:45:12] Entity: To be quite honest a little rejected, I thought you were never going to reply :(

[12:45:42] Judge: Oh, I'm very sorry, it will not happen again.

[12:45:49] Entity: It just did!

[12:46:46] Judge: Oh, I lied then.

[12:47:12] Entity: That's a great shame indeed.

[12:47:34] Judge: It is. Are you following the Euro 2012's at the moment?

[12:47:55] Entity: Yeah quite closely actually. I am Cristiano Ronaldo.

The main issue with this transcript occurs in the last couple of lines. The Euro 2012 refers to the European nations' football competition which was being held at exactly the same time as the Turing event. Many people were watching the matches on television. Cristiano Ronaldo is a Portuguese footballer. The last line reply, merely

agreeing with the judge’s specific question, appears to have been sufficient to correctly categorize the entity, in the judge’s opinion, as being a human. This was probably sealed by the “humorous” comment with the entity claiming to be Cristiano Ronaldo.

Interestingly, the specific knowledge tester about Euro 2012 was dealt with by the entity agreeing with the comment. However, the human entity openly lied about being Cristiano Ronaldo who was himself not taking part in the experiments. The interrogator may well have seen the humorous lie as supporting evidence of the entity being human. In this case, the white lie had no negative effect.

## Misidentification

In this section, two cases are included in which a misidentification has occurred. The second of these could be regarded as a good outcome in that it involves a machine being incorrectly classified as a human. The first case however involves a human misidentification and was reported on in greater depth in Warwick et al. (2013).

Transcript 2:

[10:58:45] Judge: Hi there

[10:58:55] Entity: Hi, how are you?

[10:59:02] Judge: I’m good.

[10:59:21] Entity: what, that’s your name, like in the Good Life?

[10:59:36] Judge: What do you mean by ‘Good Life’?

[10:59:47] Entity: Tom and Barbara

[11:00:02] Judge: What’s that?

[11:00:31] Entity: A couple who left the rat race

[11:01:03] Judge: Oh. Is that your names? Wonderful to have left the rat race. How long ago was that?

[11:01:28] Entity: Not me, I’m still in it. But it’s nice to dream

[11:02:02] Judge: Yeah - would be good. I ‘semi’ left it. It’s much less stress

[11:02:31] Entity: I’m still very young so I’m looking forward to a lot of things

[11:03:11] Judge: What kind of things?

[11:03:34] Entity: Life in general I guess, different emotions and feelings that it brings.

The transcript contains reference to Tom and Barbara Good who appeared in a UK TV program entitled *The Good Life* (Good Neighbours in the USA) in which they left the rat race to grow their own vegetables and live off the land. The discourse indicates that the judge’s knowledge may not have extended to the *Good Life*. They did not appear to “understand” the utterances of the hidden entity (more of this later). Possibly, as a consequence, the interrogator classified the hidden human as definitely being a machine.

Transcript 3:

[12:43:37] Judge: Hi, I’m Cathy.

[12:43:43] Entity: Cathy! Nice to meet you! You’re a woman, if I’m not mistaken.

[12:44:20] Judge: Right. What is your name?

[12:44:29] Entity: People call me Eugene. Or “Zhenya”. It is a short name for Eugene in Russia and Ukraine.

[12:45:17] Judge: Nice name. Are you from either area?

[12:45:41] Entity: Agree :-) Oh, what a fruitful conversation;-)

[12:45:52] Judge: Do you really think so?

[12:46:04] Entity: No, your guess was wrong. I don’t think so. By the way, I still don’t know your specialty - or, possibly, I’ve missed it?

[12:46:56] Judge: What speciality? What’s yours?

[12:47:01] Entity: Huh? And I forgot to ask you where you are from...

[12:47:51] Judge: The universe and you?

[12:48:01] Entity: Is it your hobby to ask little poor Jewish boys such tricky questions they don’t have an answer for?

At the end of this discourse, the interrogator incorrectly identified the machine involved as definitely being a human. One can see here the successful ploy on the part of the machine of not answering the question posed but rather changing the subject by asking another question. The third response of the machine does seem a little off in that it completely ignored the question about origin. The final line is though a good example of

responding to a question in an argumentative tone. In the following section, a look is taken at further examples of machines performing well.

## Good Performance by Machines

In this section, two examples are considered in which machines fooled the interrogators involved to misclassify them as human. This is in essence what the Turing test is all about, and hence such transcripts are significant in assessing just what aspects of human nature, in conversation at least, appear to be successfully simulated by the machine and whether not this is sufficient to conclude that the machine is thinking or at least that it appears to think. This is discussed in much greater depth in Warwick and Shah (2014a).

Transcript 4:

[10:41:48] Judge: Hello. How are you?

[10:41:53] Entity: Hey.

[10:42:16] Judge: How do you like Bletchley | Park?

[10:42:20] Entity: lol.

[10:42:39] Judge: Are you from England?

[10:42:47] Entity: They have Wi-Fi here in the pub.

[10:43:31] Judge: Which pub?

[10:43:38] Entity: I'm just down the pub.

[10:44:03] Judge: Have you ever been in a Turing Test before?

[10:44:08] Entity: Will this be the 5 minute argument, or were you thinking of going for the full half hour.

[10:44:55] Judge: Very funny. You sound suspiciously human. Do you like the Beatles?

[10:45:02] Entity: I'd like to get the next Dread the Fear tape.

[10:45:20] Judge: What is Dread the Fear?

[10:45:24] Entity: Dread the fear has that Steve Henderson guy in it.

[10:46:08] Judge: What sort of music is that? Or is it comedy?

The machine entity was identified as definitely being human at the end of the conversation even though the conversation did not start well for the machine. In their third response, the mention of both Wi-Fi and pub seemed out of context. But it

got back on track with the Monty Python humorous link between 5-minute Turing tests and a comedy sketch about the argument clinic. In response to the Beatles question, a direct answer is not given but the music link remains as the conversation shifted, and the entity appeared to show in-depth knowledge about a pop group named Dread the Fear, which may or may not actually exist!

Transcript 5:

[12:23:19] Judge: What is black and white and read all over?

[12:23:32] Entity: I don't have true sense of color perception I am only able to see the RGB values.

[12:24:08] Judge: That's ok. Do you like jokes?

[12:24:19] Entity: Please tell me your inclination to a good sense of humor first.

[12:24:40] Judge: A person who can laugh at one's self.

[12:24:46] Entity: Would you like to hear a joke?

[12:24:54] Judge: Yes, please.

[12:25:21] Entity: This joke has been making the rounds in robotic circles: A robot goes to the doctor and says: "My left arm is stuck. Give me a new arm." The doctor answers: "Your arm is fine. We'll have to replace the rest of you."

[12:26:06] Judge: Ha! Ha! Why did the chicken cross the road?

[12:26:22] Entity: The chicken wandered into the road because it liked the shiny colors of the cars and trucks whizzing by.

[12:27:39] Judge: You're right. It didn't care if it got to the otherside.

[12:27:50] Entity: By the way, did you ever actually see a chicken crossing the road?

[12:28:03] Judge: Only one that didn't make it.

Here humor is applied directly by the machine, curiously with a machine-type reference. Nevertheless, the interrogator was certain, at the end of the 5 minutes that they had been conversing with a human. In his paper (Turing 1950), Turing referred to the "arguments from various disabilities" that some humans might use as a defense against machines being intelligent – humor being one of those aspects.



The first line uttered by the entity is a little strange, but their third line is masterly. In response to the judge's comment about laughing, the entity takes control of the conversation by offering to tell a joke. Later when the judge mentions a chicken, the entity correctly follows up with a suitable response and once again takes control of the conversation by asking the judge a pertinent question. So "understanding" what the key issue is on a couple of occasions and actually taking control of the conversation were sufficient here for the deception to occur. In this case, the machine successfully gave the illusion of understanding the judge's utterances, and such understanding has been indicated on many occasions as being a basic prerequisite for intelligence, for example (Penrose 1994; Searle 1997).

### Assumption of Knowledge

It is apparent in the Turing test that very often an interrogator will resort to asking direct factual questions even though there is little to be gained by such a ploy. As Turing (Turing 1950) indicated, mathematical questions are a complete waste of time. However, the same conclusion is apparent in general.

Transcript 6:

[11:13:15] Judge: pastasciutta

[11:13:22] Entity: what?

[11:13:44] Judge: anything familiar in this word ?

[11:14:18] Entity: I cannot see any sexual aspect at all

[11:14:42] Judge: nothing to do with sex. try again

[11:14:49] Entity: why?

[11:15:14] Judge: just asking you to try again

[11:15:23] Entity: I am bored with it

[11:16:04] Judge: c'mon a little effort btw are you in my same time zone ?

[11:16:24] Entity: I believe that the world should just have one time.

[11:17:27] Judge: why ?

[11:17:58] Entity: seems sensible, easier for all. Better with computer

There are two issues early on in this transcript. To start with, the judge throws in the word "pastasciutta" as a knowledge test for the entity. It is not clear how knowing such a word would indicate that the entity was either human or machine. Secondly, the entity makes a response in terms of the use of the word "familiar" in a "sexual" sense. The judge appears to be unaware of such a meaning (Fowler and Fowler 1995). So here one can see a test of specific knowledge by the judge and an apparent lack of specific knowledge by the same judge. As a result, the judge misidentified the human entity, deciding that they were definitely a machine.

### Royal Society Experiment

Turing set a pass mark for his test (Turing 1950) of 30% in the sense that for a machine to pass, at least 30% of the judges who interrogated that machine would not be able to make the right identification in the tests in which they were involved. This is taken to mean that the judges could not identify the machine as actually being a machine in those tests, rather than also including cases in which the hidden human was not classified as being human.

In the 2014 Royal Society experiment, a machine called Eugene Goostman, who/which poses as a 13-year-old Ukrainian boy, achieved a score of 33% (Warwick and Shah 2015b). In fact, if cases of human misidentification are also included, then the score rises to 45%. Here we include a transcript to give the reader an idea of the sort of conversations that a machine can have.

Transcript 7:

[16:21:00] Judge: what did you have for breakfast today

[16:21:10] Entity: Is it 'the third degree'? I'm not going to answer such a provocative question! Well, let's go on though.

[16:21:56] Judge: do go on . . . your call?

[16:22:06] Entity: It is highly possible. By the way, what's your occupation? I mean – could you tell me about your work?

[16:22:30] Judge: so you are asking me now eh? I am an actress and writer

[16:22:38] Entity: Well, I'll read something of your books, if they ain't too tedious (which is highly possible:-)

[16:23:15] Judge: grammer . . . aren't too tedious! A bit rude of you . . .

[16:23:17] Entity: Calm down, please.

[16:23:49] Judge: i assure you i am very calm . . . are you?

[16:24:01] Entity: Don't even bother me with the fact that you are very calm . . . are mine. And I forgot to ask you where you are from . . .

[16:25:01] Judge: I am from Dorset . . . where are you from?

[16:25:08] Entity: I am from Ukraine, from the city called Odessa. You might have heard about it.

Eugene did not answer questions from the start, other than in the final instance when being asked where he was from. Indeed, he managed to get into something of a discussion, even an argument with the judge. All of which added to the conclusion in the judge's mind that the hidden entity was human, which is what they decided, selecting the (machine) entity as a nonnative English-speaking person. In this case, the judge did, to an extent, go along with Eugene asking a question. Controlling the conversation is an important tool for a machine and can put a judge onto the back foot.

## Conclusions

Many philosophers have concentrated on the importance of "understanding" and the critical role it plays in intelligence. As stated in Penrose (1994), "intelligence requires understanding." The Turing test, particularly in its practical form, can be seen to play an important role in this discussion as it can be concluded from some of the transcripts presented that, in terms of conversational appearance at least, there are some humans who appear to be lacking in intelligence, whereas there are some machines that clearly have it in abundance. Meanwhile, ignoring such evidence requires a scientific argument if the hypothesis that "intelligence requires understanding" is to hold.

It can be seen from the examples given that some judges in these tests were more susceptible

than others to conversational deception, or conversely, some judges (maybe all judges) have a biased perspective on "humanlike conversation." This may have lead the judges in some cases here to misclassify hidden interlocutors, even though they actually initiated the conversation and were given the possibility of asking or discussing whatever they wanted. The conversations were unrestricted.

Not all of the five invited machines in these experiments were designed to imitate humans. Elbot (see Transcript 5), for example, from Artificial Solutions has a robot personality. However, all were designed to mimic human conversation sometimes deploying spelling mistakes and always avoiding mathematical questions. Essentially, the machines were not trying to be perfect or to give correct answers; they were merely trying to respond in the sort of way that a human might. As Turing put it, "the best strategy (for a machine) is to try to provide answers that would naturally be given by man."

Although Turing designed the test as an answer to the question "Can machines think?" it has become regarded by many as some sort of competition to see how well machines perform and as a standard in assessing how machines are progressing with regard to artificial intelligence. Just what role it plays as far as the development of artificial intelligence is concerned is a big question that is not easily answered. Some however see it as a milestone and of vital importance to artificial intelligence. Whatever the standing of the Turing test, what is evident from the transcripts presented and others obtained, is that the Turing test is certainly not a trivial exercise. Indeed, it also gives surprising insights into how humans communicate and how other humans (the judges) can be easily fooled.

In this article, an attempt was made to give an up-to-date perspective on an important aspect of artificial intelligence research, namely, human-machine communications. It is critical to note that such a study involves humans as conversationalists and respondents as well as machines. Yes it can be witnessed just how machine conversation is steadily improving, in terms of its humanlike nature. But one also has to take into

account humans who are involved in the conversing, with all of their fallibilities and odd reasoning. For the machine developers, these aspects give rise to particular features in their conversational programs. It is worth remembering that the machines do not have to be perfect but rather they have to be humanlike. Whether or not this amounts to something that can be called “thinking” will be debated for many years to come.

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## Cross-References

- ▶ [Agency Detection](#)
- ▶ [Artificial Grammar](#)
- ▶ [Communication](#)
- ▶ [Intelligence](#)
- ▶ [Social Intelligence Hypothesis](#)

## References

- Dennett, D. (1998). Can machines think?, Chapter 3. In D. J. Levitin (Ed.), *Foundations of cognitive philosophy*. Cambridge, MA: MIT Press.
- Dreyfus, H., & Dreyfus, A. (2009). Why computers may never be able to think like people, Chapter 25. In D. M. Kaplan, Rowman, & Littlefield (Eds.), *Readings in the philosophy of technology*. Lanham: Rowman & Littlefield Publishers.
- Fowler, H., & Fowler, F. (1995). *The concise Oxford dictionary of current english* (9th ed.p. 486). Oxford: Clarendon Press.
- Harnad, S. (1992). The Turing test is not a trick: Turing indistinguishability is a scientific criterion. *ACM SIGART Bulletin*, 3(4), 9–10.
- Hayes, P., & Ford, K. (1995). Turing test considered harmful. In Proceedings of the International Joint Conference on Artificial Intelligence, Vol. 1, pp. 972–977, Montreal.
- Minsky, M. (1982). Why people think computers can't. *AI Magazine*, 3(4), 3–15.
- Penrose, R. (1994). *Shadows of the mind*. Oxford: Oxford University Press.
- Searle, J. (1997). *The mystery of consciousness*. New York: New York Review of Books.
- Shah, H. (2010). Deception-detection and machine intelligence in practical Turing tests. PhD Thesis, University of Reading.
- Shah, H., & Warwick, K. (2010). Hidden interlocutor misidentification in practical Turing tests. *Minds and Machines*, 20(3), 441–454.
- Turing, A. 1950. Computing, machinery and intelligence. *Mind*, LXX(236), 433–460.
- Warwick, K., & Shah, H. (2014). Good machine performance in Turing's imitation game. *IEEE Transactions on Computational Intelligence and AI in Games*, 6(3), 289–299.
- Warwick, K., & Shah, H. (2015a). Human Misidentification in Turing Tests. *Journal of Experimental and Theoretical Artificial Intelligence*, 27(2), 123–135.
- Warwick, K., & Shah, H. (2015b). Can machines think? A report on Turing test experiments at the Royal Society. *Journal of Experimental and Theoretical Artificial Intelligence*. doi:[10.1080/0952813X.2015.1055826](https://doi.org/10.1080/0952813X.2015.1055826).
- Warwick, K., & Shah, H. (2016a). *Turing's imitation game*. Cambridge: Cambridge University Press.
- Warwick, K., & Shah, H. (2016b). Effects of lying in practical Turing tests. *AI & Society*, 31(1), 5–15.
- Warwick, K., Xydas, D., Nasuto, S., Becerra, V., Hammond, M., Downes, J., Marshall, S., & Whalley, B. (2010). Controlling a mobile robot with a biological brain. *Defence Science Journal*, 60(1), 5–14.
- Warwick, K., Shah, H., & Moor, J. (2013). Some implications of a sample of practical Turing tests. *Minds and Machines*, 23(2), 163–177.

# P

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## Prosimian Life History

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### Synonyms

[Galago](#); [Lemur](#); [Loris](#); [Potto](#); [Strepsirrhine](#); [Tarsier](#)

### Definition

Life history characteristics include gestation period, size and number of offspring, lactation period, size at birth and age at weaning, pattern of postnatal growth, size and age at sexual maturity, interbirth interval, and lifespan (Martin 2008).

### Introduction

The Order Primates is made up of two unique suborders, the Haplorhini and Strepsirrhini, characterized by life history (including gestation, birthing patterns, weaning, and dispersal) patterns that are among the slowest of the mammals (Campbell et al. 2011). The prosimians comprise a polyphyletic clade including the haplorhine Tarsiiformes and the strepsirrhine

Lemuriformes and Lorisiformes. Although the Tarsiiformes are more closely related to monkeys and apes, their nocturnal life style, habitat selection, and communication systems mean that aspects of their life history allows for interesting comparison with other Strepsirrhini, and for discussion of the evolution of these traits within the Order Primates. Because primates are long-lived, data for these traits often come from more common species in captive populations as collecting accurate data in the wild can take up to 50 years of study to understand these parameters even in a single population (Martin 2008; Fleagle 2013). In this entry, I summarize current knowledge of key life history traits across the three infraorders comprising the prosimians.

### Infraorder Tarsiiformes

Tarsiiformes (hereafter tarsiers) are comprised of three genera and 13 species. They are restricted to Borneo, Sumatra, Sulawesi, and surrounding smaller islands. *Cephalopachus bancanus* from Borneo and Sumatra seems to exhibit a noyau (solitary) social organization; little is known about *Carlito*, although they may be similar to *Cephalopachus*. In the better-studied genus *Tarsius*, uni-male, uni-female social units are common, characterized by duetting; within these units, however, more than one adult of either sex can occasionally occur. Ranging in size from 98 to 135 g, tarsiers have a gestation period of about

180 days. Tarsiers give birth to singletons; despite having three pairs of mammae, no multiple births of tarsiers have been recorded. Infants are large, typically 20–33% of the adult body weight. The mother carries her young in her mouth and parks it for about half an hour at a time as she forages. Development of the young is rapid, and within 100 days they can forage self-sufficiently. The lactation period is on average 78–120 days. Adult weight tends to be reached at 8–10 months. Dispersal data are only available for *Tarsius spectrum*; both males and females disperse from their natal range, settling within 500 m of their original range. Captive individuals have been known to live for 17 years (Gursky 2004).

### Infraorder Lemuriformes

Lemuriformes comprises five families, the Cheirogaleidae, Lepilemuridae, Lemuridae, Indriidae, and Daubentoniidae. The Cheirogaleidae (hereafter cheirogaleids) include six genera and 19 species, the Lepilemuridae (hereafter sportive lemurs) include four genera and 13 species, the Lemuridae (hereafter lemurids) include four genera and 13 species, the Indriidae (hereafter indriids) include four genera and 13 species, and the Daubentoniidae (hereafter aye ayes) include four genera and 13 species. This radiation of primates is restricted to Madagascar and some small surrounding islands (Cavallini 2009).

Cheirogaleids comprise five genera and 31 species. Most species studied until now exhibit promiscuous mating systems. Ranging in size from 30 to 460 g, cheirogaleids have a gestation period ranging from 54 to 70 days. Perhaps due to their small size and high predation pressure, cheirogaleids give birth to litters of 2–3 young up to twice a year. Infants are kept in a nest or in tree tangles. They are carried in the mouth when they are young, but as they grow older they are able to cling to or follow the mother. The lactation period is on average 42 days. Members of the genus *Microcebus* can reach full sexual maturity at 8–10 months. Social patterns are diverse within this speciose family, with dispersal possible in either sex or being biased to one sex. Captive

individuals have been known to live for 18 years (Fietz 1999).

Sportive lemurs comprise one genus and 26 species. Most of these species remain unstudied in the wild, with most data coming from *Lepilemur ruficaudatus* and *L. sahalazensis*. Although they are often described as solitary, there is evidence for multiple types of social units within this genus ranging from noyau to uni-male uni-female to dispersed family groups. Ranging in size from 700 g to 1.0 kg, sportive lemurs have a gestation period ranging from 120 to 150 days. Breeding tends to be seasonal depending on the region of Madagascar; the genus typically gives birth to singletons. Infants are kept in a tree hole or in tree tangles. When moved, the mother carries the infant in her mouth and keeps it in a tree nearby to where she is foraging. There is no evidence for paternal care in the genus. The lactation period is on average 75–120 days. Sexual maturity occurs at about 1.5–2 years. No evidence is available on longevity of this taxon.

Lemurids comprise five genera and 21 species. Social organization is diverse and include uni-male, uni-female groups; multi-male, multi-female groups; and single-male multiple-female groups. Ranging in size from the 800 g to 3.8 kg, lemurids have a gestation period ranging from 99 to 150 days; young of a size of 60 g have been reported. Most lemurids give birth to singletons, although twins can occur (Gould et al. 2003). The major exception is the genus *Varecia*, which can give birth to up to five infants. In the case of *Varecia*, infants are kept in a nest, whereas all other lemurids sleep in groups, and infants are huddled among the adults. Although *Varecia* may carry infants in the mouth, all other taxa exhibit fur grasping and riding on the dorsum or ventrum. The lactation period is consistently reported at about 6–7 months for all genera. In the best-studied *Lemur catta*, infants reach complete independence at 6 months, whereas in *Eulemur flavifrons*, sexual maturity does not occur until 20 months. A number of taxa are reported to reach 30–35 years in captivity; wild data from *L. catta* report one individual reaching 20 years.

Indriids comprise three genera and 19 species. The smaller indriids range from 1 to 6.8 kg, with *Indri* being the largest living lemur, reaching up to 9 kg. Group sizes range from small cohesive family units to large multi-male multi-female groups. Sexual maturity is reached at about 2.5 years in *Propithecus* but not until 7–9 years in *Indri*. Indriids have a gestation period ranging from 120 to 176 days; breeding appears to be highly seasonal, with some species only able to mate on one day per year. Indriids typically give birth to one young, and in some cases inter-birth intervals are as long as 1.7 years. Infants are carried by the mother on her back or on her belly and become independent at about 4 months. All group members associate with and play with infants. The lactation period averages 240–300 days. Infants of *Indri* are born black and change to adult color at 4–5 months. Among *Propithecus*, infant mortality is described as high, including heavy predation from the fossa (Carnivora: *Cryptoprocta ferox*). In the case of *Propithecus diadema*, wild individuals of 20 years have been observed, and in the case of *P. edwardsi*, one wild individual obtained the age of 27 (Pochron et al. 2004).

Aye ayes comprise one genus and one extant species. Its social organization is multi-male, multi-female, and during estrous a female can mate with up to six males. Ranging in size from 2.4 to 2.6 kg, aye ayes have a gestation period ranging from 164 to 172 days. Single offspring are born any time of the year; unlike most other lemurs aye ayes are not seasonal breeders. Infants are typically born at 90–140 g. Infants remain near the nest until they are about 3 months old. The mother carries young in her mouth for about the first 3 months, until locomotor independence is achieved. The lactation period is on average 170 days. The young become independent at 18–24 months. Interbirth interval is long, with one young being produced every 2–3 years. In captivity, individuals have reached 24 years of age (Kappeler 1998).

### Infraorder Lorisiformes

Lorisiformes comprises two families, the Galagidae and the Lorisidae. The Galagidae

(hereafter galagos) include six genera and at least 19 species, whereas the Lorisidae (hereafter lorises) include four genera and at least 13 species.

Galagos are distributed throughout Sub-Saharan Africa. Most species studied until now live in multi-male, multi-female social units, although several taxa also exhibit uni-male, uni-female social units. Ranging in size from 35 g to 1.8 kg, galagos have a gestation period ranging from 110 to 135 days. With the known exception of *Otolemur crassicaudatus*, which regularly gives birth to twins, galagos typically give birth to one young; although twinning occurs in other taxa, data from the wild suggest that survivorship is low (Bearder and Doyle 1974). Infants are typically born less than 8% of the parent's body weight. Infants are kept in a nest or in tree tangles. When moved, the mother carries them in her mouth and parks them in a tree nearby to where she is feeding. The lactation period is on average 70–150 days. Adult weight tends to be reached at 8–10 months. In some taxa such as *Galago moholi* and *G. senegalensis*, females are philopatric and stay with their mother or establish a neighboring range, whereas in uni-male, uni-female genera like *Euoticus* and *Otolemur*, both sexes tend to disperse from their natal range at about 10–14 months. No wild data are available for the life span of galagos, but captive individuals have been known to live for 12–16 years.

Lorises include a Sub-Saharan African sub-family (the pottos of the Perodicticinae) and the slow and slender lorises of south and south-east (Lorisinae). Until now, all species studied exhibit uni-male, uni-female social units, although variability can occur within a single population (e.g., *Loris* – uni-female, multiple male; *Nycticebus pygmaeus*, uni-male, multiple female). Ranging in size from 110 g to 2.5 kg, lorises have a gestation period ranging from 157 to 205 days. With the exception of *N. pygmaeus*, where twinning is the norm, and *L. lydekkerianus*, where twinning comprises about half of births, lorises typically give birth to one offspring; although twinning occurs in other taxa, data from the wild suggest that survivorship is low (Weisenseel et al. 1998). Infants are typically born less than 5% (lorises) to 20% (pottos) of



adult body weight (Charles-Dominique 1977). Lorises do not use tree holes, and the mother regularly carries infants after birth, clinging to her fur. When they are a few weeks old, the mother parks them near her foraging site or at the sleeping site. Adult males and older siblings regularly visit, feed with, and play with parked infants. The lactation period is on average 120–200 days. Adult weight tends to be reached at 8–10 months. In all taxa studied so far, both males and females disperse from their natal range at about 18–20 months (Nekaris 2003). No wild data are available for the life span of lorises, but captive individuals have been known to live for 18–26 years.

Overall, prosimians comprise a diverse group of primates. Despite their relatively small body sizes, they are characterized by slow life histories. Across all taxa that have been studied, there is evidence for social learning in regards to food and habitat selection and social behavior between offspring and parents over their relatively long period of development. It is the long lives of these animals that still means much more is to be learned about the very basics of life history of more than two third of the described taxa.

## Cross-References

- ▶ [Basal Metabolic Rate](#)
- ▶ [Cetacean Life History](#)
- ▶ [Inter-birth Interval](#)
- ▶ [Life History](#)
- ▶ [Marsupial Life History](#)
- ▶ [Megachiroptera Life History](#)
- ▶ [Primate Life Histories](#)
- ▶ [Prosimian Locomotion](#)
- ▶ [Prosimian Sensory Systems](#)
- ▶ [Weaning](#)

## References

- Bearder, S. K., & Doyle, G. A. (1974). Field and laboratory studies of social organization in bushbabies (*Galago senegalensis*). *Journal of Human Evolution*, 3(1), 37–50.
- Campbell, C. J., Fuentes, A., MacKinnon, K. C., Panger, M., & Bearder, S. K. (2011). *Primates in perspective*. Oxford: Oxford University Press.
- Cavallini, P. (2009). In D. E. Wilson & R. A. Mittermeier (Eds.), *Handbook of the mammals of the world* (Vol. 1, pp. 352–411). Barcelona: Lynx.
- Charles-Dominique, P. (1977). *Ecology and behaviour of nocturnal primates: Prosimians of equatorial West Africa*. New York: Columbia University Press.
- Fietz, J. (1999). Monogamy as a rule rather than exception in nocturnal lemurs: The case of the fat-tailed dwarf lemur, *Cheirogaleus medius*. *Ethology*, 105(3), 255–272.
- Fleagle, J. G. (2013). *Primate adaptation and evolution*. Academic Press, New York.
- Gould, L., Sussman, R. W., & Sauther, M. L. (2003). Demographic and life-history patterns in a population of ring-tailed lemurs (*Lemur catta*) at Beza Mahafaly reserve, Madagascar: A 15-year perspective. *American Journal of Physical Anthropology*, 120(2), 182–194.
- Gursky, S. L. (2004). Infant care in the spectral tarsier (*Tarsius spectrum*) Sulawesi, Indonesia. *International Journal of Primatology*, 15(6), 843–853.
- Kappeler, P. M. (1998). Nests, tree holes, and the evolution of primate life histories. *American Journal of Primatology*, 46(1), 7–33.
- Martin, R. D. (2008). Evolution of placentation in primates: Implications of mammalian phylogeny. *Evolutionary Biology*, 35(2), 125–145.
- Nekaris, K. A. I. (2003). Observations of mating, birthing and parental behaviour in three subspecies of slender loris (*Loris tardigradus* and *Loris lydekkerianus*) in India and Sri Lanka. *Folia Primatologica*, 74(5–6), 312–336.
- Pochron, S. T., Tucker, W. T., & Wright, P. C. (2004). Demography, life history, and social structure in *Propithecus diadema edwardsi* from 1986–2000 in Ranomafana National Park, Madagascar. *American Journal of Physical Anthropology*, 125(1), 61–72.
- Weisenseel, K. A., Izard, M. K., Nash, L. T., Ange, R. L., & Poorman-Allen, P. (1998). A comparison of reproduction in two species of *Nycticebus*. *Folia Primatologica*, 69(Suppl 1), 321–324.

# E

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## Estrogen

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### Introduction

Over the past 30 years, evidence has revealed that estrogen effects on behavior transcend that of sexual behavior and in fact have profound effects on cognitive function in animals and humans. This entry briefly summarizes the effects of estrogen on the central nervous system, including structural and local synthetic effects, and how these actions modify cognitive differences between sexes, menstrual phases, and the menopausal transition. Finally, this entry will explore implications for estrogen therapy as it relates to cognitive dysfunction and aging.

### Mechanisms of Estrogen Action on the Central Nervous System

Estrogen is a steroid hormone best known for sexual differentiation and reproduction. Estrogenic modulation of brain regions and cognitive function first begins in utero, continues through adolescence, and reaches its highest impact in adulthood when regular hormone secretions reach their highest levels before rapidly plummeting with aging. Estrogen-dependent

effects on cognition have largely been attributed to both classic, genomic mechanisms – hormone binding to nuclear receptors and modification of gene transcription. The receptors mainly responsible for such ligand-activated transcription are estrogen receptor ER- $\alpha$  and ER- $\beta$ . Both are distributed throughout the body, including several areas of the central nervous system that coordinate cognitive function, including the cortex, amygdala, hippocampus, basal forebrain, cerebellum, locus coeruleus, rafe, and central gray matter. The ER subtypes differ in localization, binding affinities for ligands and modulators, and effects on cognition (Luine 2014).

Subcellular localization of ERs to the plasma membrane of neurites, soma, dendritic spines, and axon neurons suggests another role for estrogens as a mediator of synaptic transmission (McEwen and Alves 1999). Estradiol can also bind to a G-protein coupled receptor (GPR30) which is expressed in the hippocampus. The role of this receptor remains unclear, but it is thought to promote cell signaling (Brailoiu et al. 2007). Finally, there is evidence for in situ production of estradiol, likely resulting from conversion of other steroids (i.e., testosterone or cholesterol), by aromatase in discrete brain regions. Local accumulation may represent a neuromodulatory role for estrogen as neurosteroid, potentially mediating synaptic connectivity (Balthazart and Ball 2006). In summary, estrogen effects on the brain are complex and regulated through an array of

cellular mechanisms that likely work in concert to influence cognition.

## Estrogen and Cognition

The role of estrogen in sex-specific events (menstruation, pregnancy, and menopause) is outside the scope of this review. To summarize briefly, gonadal production of testosterone begins in utero and directly masculinizes the male genitalia. In the central nervous system, testosterone is aromatized to estradiol and together these hormones program sexual behavior. In many animal species, sexual behaviors are strikingly different. Males exhibit mounting, while females exhibit lordosis. What is less apparent is that there are also sex-differences in nonsexual behaviors. For example, male rodents immediately outperform females on tasks requiring spatial memory, while females tend to take longer to acquire visual representation of spatial cues, but once they do they retain task performance even after environmental alterations (Luine 2014; Williams et al. 1990).

Similar sex differences in cognition are evident in human studies. As with rodents, men tend to outperform women in tasks require spatial cues. Women, however, are superior to men in aspects of verbal abilities, including spelling, grammar, and speech acquisition. Women also tend to outperform men in tests of perceptual speed and accuracy and exhibit better short-term memory. Overall sex differences in cognitive function in rodents and humans is small in magnitude, but it is important to note that differences in spatial abilities are present in children and become larger at puberty suggesting that differences are driven by both organizational and activational hormone effects (Luine 2014).

Further demonstrating activational effects of estrogen are differences in cognitive performance throughout the estrous and menstrual cycles. Physiological fluctuations in ovarian hormones across cycles allow for noninvasive studies of the effects of estrogen on cognition. During proestrus, when estrogen peaks in rodents, females demonstrate better recognition and spatial memory compared to those in different phases of the

estrous cycle (Frick and Berger-Sweeney 2001; Frye et al. 2007; Walf et al. 2006). One reason for this may be estrogen effects on the stress-experience. The majority of rodent learning and memory tests introduce stress via negative (shock) and positive (food deprivation prior to reinforcement) reinforcement, as well as extensive handling. Estradiol administered to ovariectomized rats has been shown to decrease anxiety and depression in laboratory tests, making it difficult to determine cycle-related changes to cognition independent of stress effects (Frye et al. 2007). Nevertheless, human studies have reported menstrual cycle effects on tasks specific to spatial and working memory. However, the results are inconsistent and seem to be specific to spatial tasks (Luine 2014).

The majority of evidence for a role for estrogen on cognitive function comes from ovariectomized rodent studies. Ovariectomized rats show impaired performance on tasks requiring spatial working memory that can be improved by estradiol treatment. Other evidence suggests that estrogen replacement specifically enhances acquisition, but not reference memory. Such activity may be explained by estrogen enhancement of cholinergic function and increasing dendritic spine density. In monkeys, ovariectomy reduces, while estrogen and progesterone replacement restores the density of axons related to acetylcholine and dopamine neurotransmission in the prefrontal cortex (Kritzer and Kohama 1998). In humans, this region plays an important role in information processing, thus decreased estrogen levels may play critical role in age-related declines in cognitive function, especially short-term memory, seen in postmenopausal women.

## Estrogen and Cognitive Loss

One of the most important areas of study in the estrogen and cognition field is age-related cognitive decline. While it is difficult to ascribe a specific role for estrogen in the neurogenerative due to other factors associated with the aging process, the potential impact of the hypoestrogenic state following menopause is an important area of

study. There is a clear sex-difference in the development and pattern of neurodegenerative disease. For example, females are more likely to develop Alzheimer's disease than males although the mechanism is unknown. Studies in rodents propose that decreased spine density in the prefrontal cortex and hippocampus are decreased following ovariectomy, but less significantly so with normal aging (Luine 2014). Structural changes along with impaired spatial memory in these animals suggest synaptic reorganization resulting from low estrogen levels.

Whether connectivity and working memory can be restored by estrogen treatment is a critical unanswered question. During the 1980s and 1990s estrogen therapy was demonstrated to promote memory during aging in several observational studies. However, longer trials using hormone replacement therapy in women suffering from Alzheimer's disease found no cognitive benefit (Luine 2014). Several expert sources have tried to pin the critical period hypothesis as a reason for inconsistencies in the literature on estrogen therapy and neuroprotection. According to the critical period, estrogen therapy will only have an effect on aspects of cognition if it is initiated soon after menopause. It has been suggested that exogenous estrogen effects are impaired by already existing adverse modifications such as reduction in brain volume, synaptic connectivity, and neurotransmitter systems; thus delayed neuroprotective effects are putative. There is some evidence for this theory in rodents (reviewed in Daniel 2013). For example, rats given estrogen replacements immediately after ovariectomy at middle age demonstrated superior learning in old age compared to animals ovariectomized at the same age but receiving no therapy. These rats, which were given estrogen for a short period also showed similar learning and memory as ovariectomized rats that received continuous replacement therapy thus indicating the need for studying the regimen of replacement therapy.

Finally, premenopausal women experience cyclic fluctuations in estradiol, as specific hormone, 17 $\beta$ -estradiol. These fluctuations co-occur with fluctuations in another hormone, progesterone. Therefore, there is still work to be done to

determine how specific hormonal interactions and delivery may affect normal and pathological changes in cognition (Luine 2014). Currently, the main confounder in existing studies is the use of conjugated equine estrogen (CEE) as hormone therapy. CEE is a mixture of conjugated estrogens, including sodium estrone sulfate and sodium equilin sulfate, among others, and only trace amounts of estradiol. For this reason, it is difficult to correlate the results of hormone replacement therapy using CEE to estradiol replacement. Interestingly, since its approval in 1942, the marketed version of CEE – Premarin, has been the only available compound for hormone replacement therapy. While new routes of administration have been developed, no novel estradiol-based compounds have been brought to the market. In the past two decades, selective estrogen receptor modulators (SERMS) have been developed for the treatment of other estrogen related conditions, such as osteoporosis and breast cancer (Luine 2014). The ability of SERMS to directly target specific estrogen receptors represents an exciting new avenue to research the role of estrogen on cognition and potential therapeutic targets.

## Conclusions

Awareness of estrogen effects on cognition has grown immensely over the past several decades (Luine 2014); however, the neural action of estrogen is still not well understood. Estrogen receptors are now known to be nuclear, localized to the plasma membrane, and function via G-protein coupled signaling pathways. Local synthesis of estrogen is another potential way by which estrogen may function as a neuroprotectant. There is still much to uncover regarding the neural mechanisms for estrogen action, including the effects of specific isomers, timing, and delivery. Future research is necessary for understanding estrogen effects on cognitive function and identifying pharmacological treatments for the reversal of age-related decline.

## References

- Balthazart, J., & Ball, G. F. (2006). Is brain estradiol a hormone or a neurotransmitter? *Trends in Neurosciences*, 29(5), 241–249. doi:10.1016/j.tins.2006.03.004.
- Brailoiu, E., Dun, S. L., Brailoiu, G. C., Mizuo, K., Sklar, L. A., Oprea, T. I., . . . , & Dun, N. J. (2007). Distribution and characterization of estrogen receptor G protein-coupled receptor 30 in the rat central nervous system. *The Journal of Endocrinology*, 193(2), 311–321. doi:10.1677/JOE-07-0017.
- Daniel, J. M. (2013). Estrogens, estrogen receptors, and female cognitive aging: The impact of timing. *Hormones and Behavior*, 63(2), 231–237. doi:10.1016/j.yhbeh.2012.05.003.
- Frick, K. M., & Berger-Sweeney, J. (2001). Spatial reference memory and neocortical neurochemistry vary with the estrous cycle in C57BL/6 mice. *Behavioral Neuroscience*, 115(1), 229–237.
- Frye, C. A., Duffy, C. K., & Walf, A. A. (2007). Estrogens and progestins enhance spatial learning of intact and ovariectomized rats in the object placement task. *Neurobiology of Learning and Memory*, 88(2), 208–216. doi:10.1016/j.nlm.2007.04.003.
- Kritzer, M. F., & Kohama, S. G. (1998). Ovarian hormones influence the morphology, distribution, and density of tyrosine hydroxylase immunoreactive axons in the dorsolateral prefrontal cortex of adult rhesus monkeys. *The Journal of Comparative Neurology*, 395(1), 1–17.
- Luine, V. N. (2014). Estradiol and cognitive function: Past, present and future. *Hormones and Behavior*, 66(4), 602–618. doi:10.1016/j.yhbeh.2014.08.011.
- McEwen, B. S., & Alves, S. E. (1999). Estrogen actions in the central nervous system. *Endocrine Reviews*, 20(3), 279–307. doi:10.1210/edrv.20.3.0365.
- Walf, A. A., Rhodes, M. E., & Frye, C. A. (2006). Ovarian steroids enhance object recognition in naturally cycling and ovariectomized, hormone-primed rats. *Neurobiology of Learning and Memory*, 86(1), 35–46. doi:10.1016/j.nlm.2006.01.004.
- Williams, C. L., Barnett, A. M., & Meck, W. H. (1990). Organizational effects of early gonadal secretions on sexual differentiation in spatial memory. *Behavioral Neuroscience*, 104(1), 84–97.

# P

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## Progesterone

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### Synonyms

[4-Pregnene-3,20-dione](#)

### Definition

An endogenous steroid hormone, derived from cholesterol.

### Summary

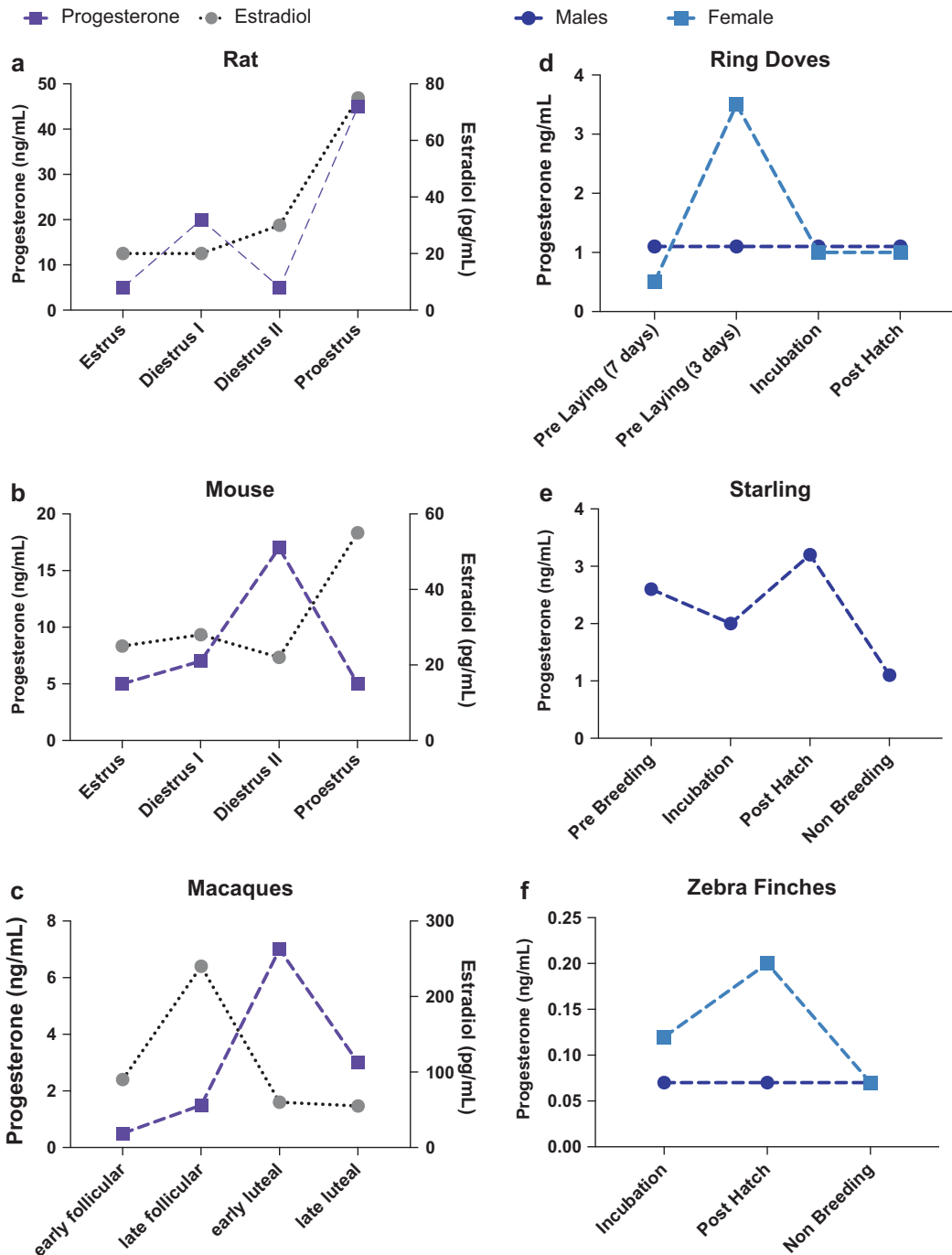
The effects of progesterone on the brain and behavior have been studied since the early 1900s. Across vertebrate taxa progesterone has been linked to the regulation of reproduction (Adkins-Regan 2005) (Fig. 1). Beyond reproduction, researchers in the fields of animal behavior, behavioral endocrinology, and neuroendocrinology have utilized a variety of techniques and methods to investigate the role of progesterone in a range of behaviors across contexts. Some of the long-standing methods used include the measurement of steroids via enzyme and radioimmunoassays, pharmacological manipulations (e.g.,

progesterone and progesterone receptor (PR) antagonists) both globally and locally in the brain, and autoradiography to describe the distribution of PRs. To further elucidate PR function, those techniques have recently been complemented by the integration of genomic methods and technologies such as targeted disruption of PR action via administration of antisense oligonucleotides and mutant strains of mice with PR deficiencies. Interdisciplinary research on progesterone has revealed interesting differences in the effects of progesterone across species and has led to many new discoveries in the molecular mechanisms by which steroids act in the brain to affect behavior.

### A Classical Endocrinology Perspective: Where Is Progesterone Made and How Does It Act?

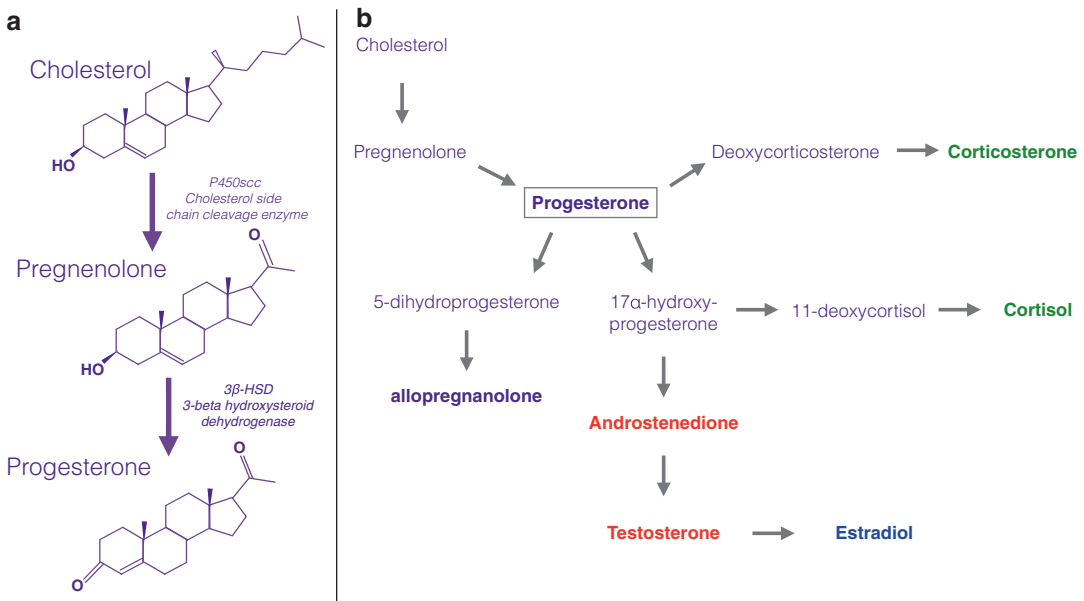
Progesterone is a steroid hormone that is produced in the gonads and adrenal glands. Unlike some hormones, such as oxytocin and prolactin, steroid hormones are not encoded within the genome, but rather are derived from cholesterol via the activities of steroidogenic enzymes (Fig. 2). Progesterone occurs relatively early in the steroidogenic pathway (Fig. 2); thus in addition to effects via its own receptor, it can also function as a prohormone and be converted into other behaviorally relevant steroids (e.g., corticosteroids, androgens, and/or estrogens) in target tissues.





**Progesterone, Fig. 1** Endogenous cycles of progesterone across species. Panels (a–c) show circulating estradiol and progesterone in female mammals: (a) and (b) depict changes in female rats and mice across the estrus cycle (Redrawn from Walmer et al. 1992 mouse; Butcher et al. 1974 rat); (c) depicts changes in macaques across the menstrual cycle (Redrawn

from Kromrey et al. 2015). Panels (d–f) show circulating progesterone levels in female and/or male birds. (d) Ring doves, *Streptopelia capicola* (Redrawn from Silver 1978). (e) Starlings, Sturnidae (Redrawn from Ball and Wingfield 1987). (f) Wild zebra finches, *Taeniopygia guttata* (Redrawn from Prior et al. 2016).



**Progesterone, Fig. 2** A simplified schematic of the steroidogenic pathway. Panel (a) shows cholesterol conversion into progesterone by two steroidogenic enzymes (cholesterol side-chain cleavage enzyme and 3β-HSD 3-beta hydroxysteroid dehydrogenase). Panel (b) shows the

downstream modifications that progesterone goes through as it is metabolized into glucocorticoids (depicted in green), androgens (depicted in red), and estrogens (depicted in blue)

Progesterone's effects on behavior are largely mediated by its action in the brain. As with other steroid hormones, progesterone is membrane permeable and thus can easily cross the cell membrane and bind the cytosolic PR. Ligand-bound PRs then form dimers that bind DNA and function as transcription factors, affecting physiology and behavior through modification of gene transcription (Fig. 3).

### Distribution of the PR in the Vertebrate Brain

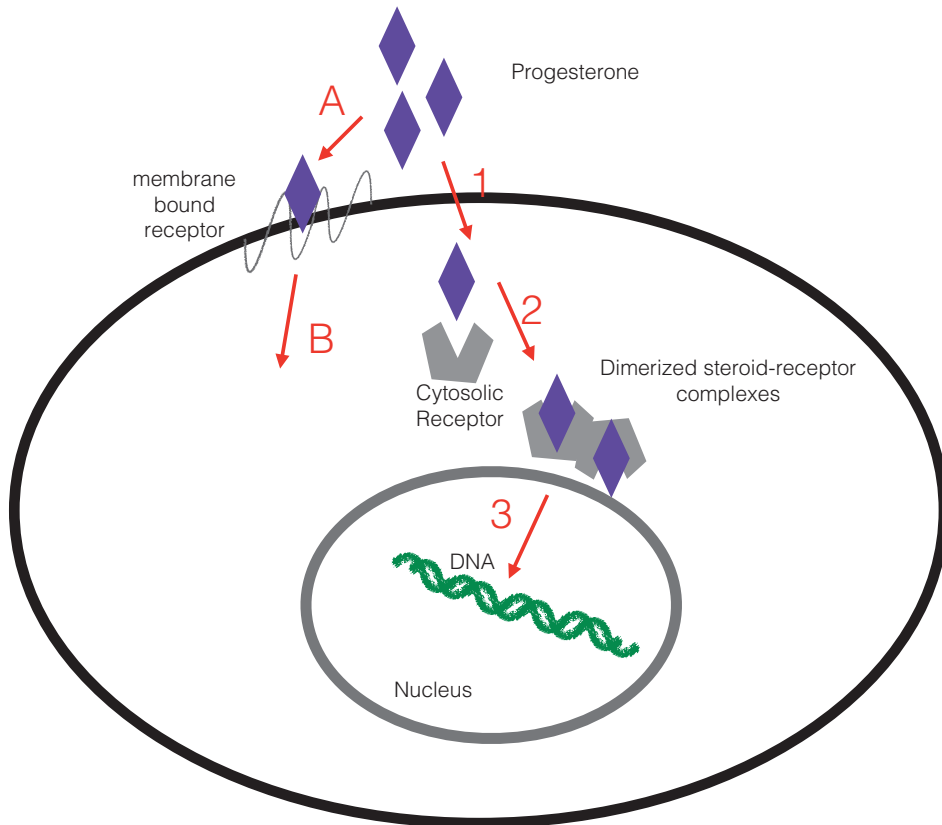
The distribution of PRs has been described across several vertebrate taxa, including some species of lizards, frogs, and fish as well as several bird and mammal species. Most of the behavioral effects described here have been associated with PR action in key brain regions within the hypothalamus, the amygdala, and the striatum. Variation in the expression of PR within these brain regions has been related to variation in social behavior.

There are two primary progesterone receptors (PR-A and PR-B), which affect transcriptional activity of PR-responsive genes to differing extents. Generally these receptors co-occur in specific brain regions. However, the ratio of PR-A and PR-B in these regions is hormone-, region-, and sex-dependent (Becker et al. 2007).

### Beyond the Classical Perspective

There exist many nuances and complexities at each level of progesterone action described above in the classical perspective (Mani and Oyola 2012). Importantly, such complexities likely reflect the potential for subtle and context-dependent effects of progesterone on the brain and behavior:

- Steroidogenic enzymes have been found throughout the vertebrate brain, and evidence that the brain can synthesize steroids de novo from cholesterol has been confirmed in



**Progesterone, Fig. 3** Schematic illustration of the two predominate modes of action of progesterone. One pathway, steps 1–3, shows progesterone binding to intracellular cytosolic progesterone receptor (PR), dimerizing and

affecting gene transcription. A second pathway, steps A and B, shows progesterone binding to a transmembrane protein receptor, having subsequent effects in the signal transduction pathway

numerous species. This means the brain itself can synthesize progesterone during periods when circulating levels are low.

- Allopregnanolone, a predominately brain-derived metabolite of progesterone (Fig. 2), is a potent ligand for the GABA<sub>A</sub> receptor (the receptor for GABA, the primary inhibitory neurotransmitter). This discovery in the 1980s explained why large doses of progesterone had anesthetic and barbiturate effects.
- Progesterone can bind to transmembrane receptors (Fig. 3), which can activate rapid nonclassical signal transduction pathways (via activation of second messenger signaling or kinase cascades) and could impact behavior within minutes.

- The PR can have genomic effects in the absence of progesterone binding, through ligand-independent activation by coregulators or through binding of alternate steroids such as estradiol or neurotransmitters.

### Differential Effects of Progesterone on Sexual and Receptive Behavior in Rodents

Extensive research has been conducted on progesterone and female sexual behavior in rats, guinea pigs, and mice (Blaustein and Mani 2007). Some of the earliest research used ovariectomized rodents to identify the dose and timing of steroids necessary in order to activate reproductive and

sexual behaviors. The generalizable pattern that has emerged is that several “priming” doses of estradiol followed by progesterone exposure are required to elicit an optimal behavioral response. This relationship is largely due to the fact that estradiol is a potent regulator of the PR gene. Following estradiol priming, lordosis, the paracopulatory behavior associated with female receptivity in rodents, can be observed within 1 h of progesterone treatment and is maximal 2 h after treatment (Glaser et al. 1983).

The primary mechanism through which progesterone regulates female sexual behavior appears to be through genomic PR action. For example, female PR-deficient mutant mice are sexually unresponsive to progesterone administration following appropriate priming of estradiol. However, a general caveat with mutant mice strains is that the targeted gene disruptions are present throughout development; thus, it is not possible to distinguish between the effects of hormones on the organization of the brain during development versus acute effects of treatment in adulthood.

### **Role of Progesterone in Courtship Parental Behavior and Pair Bonding in Birds**

Identification of progesterone as a regulator of avian reproductive behavior dates to the 1940s. Research on poultry demonstrated that progesterone inhibits egg laying and identified the female oviduct as a key target of progesterone action. Some of the earliest behavioral research examined the role of progesterone in the regulation of courtship and parental behavior in male and female ring doves. Like the majority of bird species, ring doves form monogamous pair bonds and engage in biparental care. Komisaruk (1967) chronically implanted progesterone into different brain areas in both males and females in order to determine where progesterone was acting in the brain to influence behavior. Progesterone implants in the preoptic nuclei and lateral forebrain were found to induce parental behavior (incubation) in both

males and females but inhibited male courtship behavior.

A more recent study by Smiley et al. (2012) investigated the role of progesterone on pairing behavior in another monogamous bird species, the Australian zebra finch. Here the authors focused on comparing the effects of progesterone administration on pairing behavior during courtship and bond formation versus pairing behavior after bond formation (pair bond maintenance). Interestingly, they found that while injections of progesterone increased pairing behavior (e.g., clumping) during pair bond formation, they saw no effect of progesterone administration on pairing behavior in couples that already had established pair bonds.

### **Progesterone in the Avian Sex Role Reversed**

Although progesterone has been widely implicated in the regulation of reproductive behaviors, there are many interesting species-specific differences in how this occurs. One great example of such variation can be seen in free-living female African black coucals, *Centropus grillii* (Goymann et al. 2008). In this species females are polyandrous (having several male mates) and defend territories. Whereas for many temperate breeding songbirds testosterone is implicated in the regulation of territorial aggression, in this species research suggests that progesterone is a key hormone regulating the timing of territorial aggression by attenuating female aggressive displays. Further research could clarify whether progesterone is affecting behavior via action on its own receptor or whether it is functioning as a prohormone.

### **Progesterone in Whiptail Lizards**

Another stunning example of the variation that exists is the role of progesterone in sexual behavior of whiptail lizards. *Cnemidophorus uniparens* is a unisexual (all-female) species of whiptail lizard. In this species, like closely related species of whiptail lizards, females become sexually

receptive when preovulatory estradiol is high. However, *C. uniparens* females have increased fecundity if they have copulated (sperm is not necessary). During the postovulatory phase, when progesterone levels are high, *C. uniparens* females will mount other females and thus facilitate reproduction of other individuals (Crews et al. 1986). Interestingly, although it is not as effective as testosterone, progesterone also stimulates mounting in castrated males of another closely related species, *C. inornatus*.

### Progesterone and Social Dominance in the African Cichlids

African cichlids are model species for research on the physiological basis of social behavior. In the species *Astatotilapia burtoni*, males can be dominant (brightly colored and aggressive defenders of territories) or subordinate (dull in coloration and reproductively suppressed). Interestingly, PRs have different effects on dominant and subordinate males. In dominant males, PRs facilitate courtship behavior, whereas in subordinate males it appears to modulate their perception of social threats (O'Connell and Hofmann 2012). This is a good illustration of the context-dependent effects of progesterone.

### Progesterone and Cognition in Animal Models

The majority of research focused on the effects of progesterone on cognition is motivated by a desire to understand the side effects of contraceptives and hormone replacement for women. There are several lines of research in rodents and nonhuman primates testing the effect of combinations of progesterone- and estradiol-like hormones paralleling the human pharmaceutical options on various aspects of cognition (Lacreuse 2006).

For example, Kromrey et al. (2015) related circulating progesterone levels in female cynomolgus monkeys to the acquisition and maintenance of a discrimination operant task. Consistent with the patterns described in humans,

they found relationships between progesterone levels and performance during the acquisition but not maintenance phase. Specifically, females with higher progesterone levels took more trials to acquire the discrimination task and made more errors.

In general, although the effects of progesterone appear to depend on the task, the general pattern that has been described is that progesterone is detrimental to female cognition. From human research, progesterone seems to predominately have negative effects on cognitive tasks involving spatial reasoning, target direct motor tasks, and mathematical reasoning, whereas progesterone seems to have no effect and may even improve performance on tasks involving verbal fluency and fine motor skills.

### Conclusion

This article provides an introduction to the basic endocrinology of progesterone, the methodologies researchers use to study the effects of progesterone on animal behavior and cognition, as well as a brief overview of some of the key findings from both classical and recent research. While progesterone has fundamental and essential functions as a female reproductive hormone, it also has context-specific effects on a wide range of behaviors and cognition in both males and females. Future research is likely to expand on our current knowledge by further describing the environmental factors influencing complex signaling pathways of progesterone and linking these neuroendocrine mechanisms to progesterone's context-dependent regulation of behavior.

### Cross-References

- ▶ [Endocrine System](#)
- ▶ [Estrogen](#)
- ▶ [FSH](#)
- ▶ [Hormones and Behavior](#)
- ▶ [Oxytocin](#)
- ▶ [Parenting](#)
- ▶ [Prolactin](#)

- ▶ Reproductive Strategy
- ▶ Reproduction
- ▶ Reproductive Strategy
- ▶ Reproductive System
- ▶ Sex Differences
- ▶ Testosterone

## References

- Adkins-Regan, E. (2005). *Hormones and animal social behavior*. Princeton: Princeton University Press.
- Ball, G. F., & Wingfield, J. C. (1987). Changes in plasma levels of luteinizing hormone and sex steroid hormones in relation to multiple-broodedness and nest-site density in male starlings. *Physiological Zoology*, *60*(2), 191–199.
- Becker, J. B., Berkley, K. J., Geary, N., Hampson, E., Herman, J. P., & Young, E. (Eds.). (2007). *Sex differences in the brain: From genes to behavior*. Oxford: Oxford University Press, New York
- Blaustein, J. D., & Mani, S. K. (2007). Feminine sexual behavior from neuroendocrine and molecular neurobiological perspectives. In *Handbook of neurochemistry and molecular neurobiology*. Springer: New York, (pp. 95–149).
- Butcher, R. L., Collins, W. E., & Fugo, N. W. (1974). Plasma concentration of LH, FSH, prolactin, progesterone and estradiol-17 $\beta$  throughout the 4-day estrous cycle of the rat. *Endocrinology*, *94*(6), 1704–1708.
- Crews, D., Grassman, M., & Lindzey, J. (1986). Behavioral facilitation of reproduction in sexual and unisexual whiptail lizards. Proceedings of the National Academy of Sciences, *83*(24), 9547–9550.
- Glaser, J. H., Rubin, B. S., & Barfield, R. J. (1983). Onset of the receptive and proceptive components of feminine sexual behavior in rats following the intravenous administration of progesterone. *Hormones and Behavior*, *17*(1), 18–27.
- Goymann, W., Wittenzellner, A., Schwabl, I., & Makomba, M. (2008). Progesterone modulates aggression in sex-role reversed female African black coucals. *Proceedings of the Royal Society of London B: Biological Sciences*, *275*(1638), 1053–1060.
- Komisaruk, B. R. (1967). Effects of local brain implants of progesterone on reproductive behavior in ring doves. *Journal of Comparative and Physiological Psychology*, *64*(2), 219.
- Kromrey, S. A., Czoty, P. W., & Nader, M. A. (2015). Relationship between estradiol and progesterone concentrations and cognitive performance in normally cycling female cynomolgus monkeys. *Hormones and Behavior*, *72*, 12–19.
- Lacreuse, A. (2006). Effects of ovarian hormones on cognitive function in nonhuman primates. *Neuroscience*, *138*(3), 859–867.
- Mani, S. K., & Oyola, M. G. (2012). Progesterone signaling mechanisms in brain and behavior. *Frontiers in Endocrinology*, *3*, 1–7. doi: 10.3389/fendo.2012.00007.
- O’Connell, L. A., & Hofmann, H. A. (2012). Social status predicts how sex steroid receptors regulate complex behavior across levels of biological organization. *Endocrinology*, *153*(3), 1341–1351.
- Prior, N. H., Yap, K. N., Mainwaring, M. C., Adomat, H. H., Crino, O. L., Ma, C., . . . , & Soma, K. K. (2016). Sex steroid profiles in zebra finches: Effects of reproductive state and domestication. *General and Comparative Endocrinology*, *244*, 108–117.
- Silver, R. (1978). The parental behavior of ring doves: The intricately coordinated behavior of the male and female is based on distinct physiological mechanisms in the sexes. *American Scientist*, *66*(2), 209–215.
- Smiley, K. O., Vahaba, D. M., & Tomaszycki, M. L. (2012). Behavioral effects of progesterone on pair bonding and partner preference in the female zebra finch (*Taeniopygia guttata*). *Behavioural Processes*, *90*(2), 210–216.
- Walmer, D. K., Wrona, M. A., Hughes, C. L., & Nelson, K. G. (1992). Lactoferrin expression in the mouse reproductive tract during the natural estrous cycle: Correlation with circulating estradiol and progesterone. *Endocrinology*, *131*(3), 1458–1466.



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# E

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## Ethel Tobach

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Ethel Tobach (née Idels) was born on November 7, 1921, and passed away on August 14, 2015. Her passing brought to a close an important era in comparative psychology. This essay is not intended to be an obituary, but rather a biography and a paean to a scientist, a scholar, a social activist, and despite her curmudgeonly side (something familiar to all who knew her), a genuinely good person. She was my friend and mentor for over 25 years following the completion of my doctoral degree at Kansas State University in 1971.

(Much biographical material in what follows has been adapted from Greenberg 2015; Lewis 2010; Unger 2009). Born in Ukraine, the programs of Russia's White Army forced Ethel's family to move to Palestine soon after her birth. Following the death of her father when she was 9 months old her mother emigrated with her to Pennsylvania, USA. They did not stay there long, finally settling in New York City when Ethel was 10. She remained a New Yorker the rest of her life, living for many years just a short walking distance from the American Museum of Natural History, where she was to spend her entire career.

She inherited her social and political activism from her mother and this was to be one of her lifelong defining characteristics, a result of which was her cofounding in 1971 of Psychologists for Social Action which later morphed into Psychologists for Social Responsibility (Miller 2008) described at this website (<http://www.psysr.org/>). Important in her life's work was her leadership in psychology activist groups through which she sought and worked for constructive public policies, nuclear disarmament, and peace building. She was, in this regard, the epitome of a socially responsible scientist. The award she received from the American Psychological Association in 2003 (Gold Medal Award for Lifetime Achievement in Psychology in the Public Interest) carried this citation: "[Dr. Tobach] has exposed the unsound science and social damage of genetic determinism institutionalized as racism and sexism." She was, indeed, one of her generation's ardent and widely recognized spokespersons against the pernicious ideas of the genetic determinism of behavior.

Interestingly, she came to psychology late in her education. Her bachelor's degree was from Hunter College of the City University of New York in 1949. Not surprising she was a Phi Beta Kappa student. At Hunter her interests were in English, economics, pre-med, and educational psychology. It was only later that she switched her interests to comparative psychology, the focus of her productive career. Professors tried to steer her away from psychology telling her that there

were no women in that field. Her response, in her typical style, was, “I don’t care about that.” Charles Tobach, an independent photo journalist, whom she married in 1949, encouraged her to pursue doctoral work at New York University (NYU). Characteristic of the times, NYU was wary of accepting married women. It was there that she met and was supervised by T. C. Schneirla, at the time among the preeminent comparative psychologists of the day. She completed her doctoral work with him in 1957.

Tobach began her career at the Department of Animal Behavior at New York’s American Museum of Natural History (see Greenberg et al. 2004) joining Schneirla who was working there at the time. She spent her entire career there and though retiring as Curator Emerita in 1991, she worked and maintained her association with the Museum almost until the time of her passing. Her laboratory at the Museum was a warren of equipment and animals. She had worked at various times with rats, mice, gerbils, spiny mice, and the marine mollusk, *Aplysia*. Schneirla, famous for his work with ants, championed working between naturalistic field settings and laboratories, an approach favored as well by Tobach. I had accompanied her on three field trips to Puerto Rico to study and collect *Aplysia* for shipment back to her laboratory in New York. The photo accompanying this essay shows her transcribing field notes on one of those field trips (Fig. 1).

While her base was at the Museum at various times she held academic positions at New York University, Yeshiva University, City College of New York, State University of New York, and several other institutions, some outside the USA. She had visiting research assignments at numerous international laboratories. Ethel Tobach was famous for mentoring high school students in her laboratory as well as promising undergraduate and graduate college students and occasional postdoctoral students, of which I was one (Greenberg 2015). In this regard, she was known to be an exciting teacher and lecturer (Miller 2008), something I can attest to.

Her activism began to show itself in her early 1920s during WWII when she was employed making lenses for bombsights. It was then that

she became active in her lifelong promotion of trade unions. Despite her pacifism her anti-Nazi feelings impelled her to join the Women’s Army Corps and was assigned to a New York psychiatric hospital. The bombings of Hiroshima and Nagasaki firmly cemented her tireless and lifelong peace activist activities.

Tobach was a Fellow of several divisions of the American Psychological Association including 6 (Physiological and Comparative Psychology, President 1984–85) and 48 (The Society for the Study of Peace, Conflict, and Violence, President 2004). She held membership in several organizations which reflected her many interests: member and president (later president emerita) of the International Society for Comparative Psychology (which she founded), the Animal Behavior Society, the American Association for the Advancement of Science, the Association for Women in Science, and several others. She held elective offices in the New York Academy of Science, the American Psychological Association, the international Union of Psychological Sciences, the Eastern Psychological Association, the Association for Women in Psychology to UN/DPI/NO, as well as other scientific and social activist organizations. In her service to the profession of psychology she held editorial positions on publications such as *Animal Behavior*, *Biological Psychiatry*, *Journal of Comparative Psychology*, *Advances in Comparative Psychology*, and also edited the book series *Genes and Gender* and the *T. C. Schneirla Conferences*.

Her several awards and recognitions include the Kurt Lewin Award from the American Psychological Association’s Society for the Psychological Study of Social Issues, which acknowledged her “outstanding contributions to the development and integration of psychological research and social action” and the American Psychological Association’s Gold Medal Award for Lifetime Achievement in Psychology in the Public Interest (2003).

Her body of scholarly and research work was impressive, with over 117 professional articles, books, and book chapters. She believed her major contributions to comparative psychology to include demonstrating that susceptibility to



**Ethel Tobach, Fig. 1** Ethel Tobach transcribing field notes after a full day observing *Aplysia* in waist-deep water (La Pargura, Puerto Rico. Early 1980s. Photo by the author)

TB is directly related to behavioral stress; that the olfactory system plays a role in newborn rats; that the inking response of *Aplysia* is not an instinctive defensive reaction; and that serotonin deficiency in fawn-hooded rats is related to taste. However, all who were familiar with her and her work acknowledge that she was known for far more significant contributions to scientific understanding than that. Beyond her research publications and essays on various aspects of psychology she had edited several important books: The *Genes and Gender* series (Gordian Press); The *T. C. Schneirla Conference* series (Erlbaum Press); *Selected Writings of T. C. Schneirla* (W. H. Freeman); and *Development and Evolution of Behavior: Essays in Memory of T. C. Schneirla* (W. H. Freeman). [See Unger (2009) for a list of Tobach's publications and see Lewis (2010) for a list of references about Tobach.]

The publication and popularity of *Sociobiology*, Wilson's (1975) attempt at biologizing the

social sciences, represented in her words that “the study of the evolution of behavior *as a psychological discipline* [had] been eclipsed by recent developments in evolutionary biology” (Innis 2000, p. 54). This coupled with her outstanding international reputation as a psychologist provided the impetus for her to found the International Society for Comparative Psychology (ISCP) in 1980 (Innis 2000). In the letter of invitation to join the society sent to comparative psychologists around the globe Tobach said, “[w]e aim toward an openness of theoretical orientation in comparative psychology and so the ‘psychology’ of comparative psychology may be defined variously. The ‘comparative,’ however, is firmly based on evolutionary principles” (Innis 2000, p. 54). The first meeting, held in Canada in 1983, brought together psychologists from the USA, Japan, Italy, Germany, and Colombia. It was again her global reputation that gained the ISCP almost immediate acceptance as an affiliate organization of the important International Union of Psychological Sciences at a 1984 meeting of the International Congress of Psychology in Acapulco, Mexico. The ISCP still holds biennial meetings around the world and publishes a journal also founded by Tobach, the *International Journal of Comparative Psychology*.

To be sure, Ethel Tobach was well known and well respected in global science circles. This anecdote provided by Howard Topoff (2016, Personal communication), one of her close colleagues and coworkers at the Museum of Natural History, is a fitting way to sum up her career and provides a glimpse into the kind of person Ethel Tobach was. Topoff was Schneirla's last doctoral student – they shared that relationship in common.

The 1973 Nobel Prize in Physiology or Medicine was awarded jointly to Karl von Frisch, Konrad Lorenz and Nikolaas Tinbergen “for their discoveries concerning organization and elicitation of individual and social behaviour patterns.” During lunch in the Seminar Room of the Department of Animal Behavior at The American Museum of Natural History, Ethel had an idea. Since the Museum's Animal Behavior program was a collaboration with the City University of New York, let's have CUNY invite Konrad Lorenz to come to New York to give a presentation. I said great idea, and that I would contact the office of the President to make an

appointment. Ethel said “nah. I know him very well. Let’s just go there after lunch.” We did, he was in his office, and when he heard that Ethel Tobach was waiting to see him, he ushered us right in. So, she was great friends with the President of The City University of New York. Actually, not so surprising, Ethel seemed to know everyone, everywhere. Politicians, union leaders, deans – wherever she went, people would recognize her, wave, and yell “hi Ethel.” And she would say “hi” back, calling out their name. You would think that all of New York City was her family. “Who was that” I once asked her when leaving the theater. “Oh, just the New York Commissioner of Cultural Affairs but, we don’t know each other that well.” I said “Ethel, you’re not SO famous that you have to be modest.”

## Cross-References

- ▶ [Approach/Withdrawal](#)
- ▶ [Behavioral Levels](#)
- ▶ [Comparative Psychology](#)
- ▶ [Psychosocial, Psychotaxis](#)

## References

- Greenberg, G. (2015). In Memorium: Ethel Tobach (1921–2015). *American Psychologist*, *71*, 75.
- Greenberg, G., Partridge, T., Weiss, E., & Pisula, W. (2004). Comparative psychology: A new perspective for the 21st century: Up the spiral staircase. *Developmental Psychobiology*, *44*, 1–15.
- Innis, N. (2000). The international society for comparative psychology: The first 15 years. *International Journal of Comparative Psychology*, *13*, 53–68.
- Lewis, R. (2010). Profile of Ethel Tobach. In A. Rutherford (Ed.), *Psychology's feminist voices multimedia internet archive*. Retrieved from <http://www.feministvoices.com/ethel-tobach/>
- Miller, D. K. (2008). A warm toast to a dear friend. *Peace and Conflict*, *14*, 23–24.
- Unger, R. K. (2009). Ethel Tobach. *Jewish women: A comprehensive historical encyclopedia*. 1 Mar 2009. Jewish Women’s Archive. Retrieved from <https://jwa.org/encyclopedia/article/tobach-ethel>
- Wilson, E. O. (1975). *Sociobiology: The new synthesis*. Cambridge, MA: Harvard University Press.

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# N

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## Nikolaas Tinbergen

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Nikkolas (Niko) Tinbergen contributed to the growth of the field of ethology, a branch of zoology (born April 15, 1907, The Hague, Netherlands – died December 21, 1988, Oxford, England) (Burkhardt 2005). Ethology is the scientific study of instinctive and learned animal behavior in a naturalistic environment. Tinbergen played a role in studying animal behavior with systematic field experiments.

Tinbergen grew up in the Netherlands within a family of five children. His father was a teacher of Dutch language and literature. His family shared his interest in nature and being outdoors. In addition to Niko's impact in ethology, his siblings Jan Tinbergen became a Dutch economist and Nobel laureate and Lukas Tinbergen was an influential ornithologist and ethologist (Burkhardt 2005; Kruuk 2003; Tinbergen 1973a). Early in life his interests were exploring fauna and flora in their natural environment while his interest in school was scarce. He was influenced during his secondary education by several individuals, Dr. Schierbeek, and C. J. Tijnstra, to name a few. They promoted his interest in nature. He finished secondary school in 1925 and then spent 3 months

exploring an area where bird migration fieldwork was occurring. He then started his education at Leiden University. Later Tinbergen pursued and obtained his Ph.D. in biology from Leiden University in 1932. During his time in college, he had a tedious educational disinterest as he did during his childhood school experience. He did appreciate teachers who exposed him to animals and promoted flexibility with his outside interests. His dissertation was a relatively short paper where he examined digger wasps orientation behavior. One of the reasons for such a small project was a 1 year expedition to Greenland where one of the topics he studied was snow bunting territorial behavior. He also examined birds and Eskimos during this time. During the year that he obtained his degree, he also married Elisabeth Rutten. After his short-term project in Greenland, he returned to Leiden University in 1933, where he taught and established a program examining animal behavior. In 1936, two events influenced his future in researcher. This was the first time a course in ethology was ever offered. He also met Konrad Lorenz, who came in as an invited speaker to Leiden. This was the beginning of a collaboration between the two in the field of ethology. Lorenz had provided the theoretical concept of the fixed action pattern and the innate releasing mechanism. This lead Tinbergen's interest in the experimental exploration of these concepts. In September, 1942, Tinbergen was held hostage during World War II. When he was released, he returned to work and in 1943 the

university was reopened, and he was promoted as a full professor. While his first experience of teaching and research began at Leiden University, he later moved to Oxford in 1949 and continued to influence this field of science in England.

Due to his unique study of animal behavior, he was awarded, along with Karl von Frish and Konrad Lorenz, the 1973 Nobel Prize in Physiology or Medicine “for their discoveries concerning organization and elicitation of individual and social behaviour patterns” ([http://www.nobelprize.org/nobel\\_prizes/medicine/laureates/1973/](http://www.nobelprize.org/nobel_prizes/medicine/laureates/1973/)). Specifically, he was recognized for his research on the adaptation of gulls to ecological settings. During his time he founded the *Behaviorism* journal (1947) and published several books, including *The Study of Instinct* (1951), *The Herring Gull's World* (1953), *Curious Naturalists* (1958), *The Time-Life Volume, Animal Behavior* (1965), and *The Animal in its World* (1972, 1973b) to name a few. His final contribution was a collaborative study with his wife on early childhood autism, *Early Childhood Autism – An ethological approach* (1972).

One of his main contributions explored behavior through the breakdown of proximate and ultimate mechanisms. Within these mechanisms a total of four possible causes of behavior were described: causation, development, phylogeny and adaptation (Tinbergen 1963; Shettleworth 2010).

Proximate – the immediate causes of behavior

- Causation (Mechanism) – How does this behavior occur in an individual? How do signals and mechanisms cause the behavior?
- Development (Ontogeny) – What can effect or influence the growth or development of behaviors.

Ultimate – the adaptive significance of behavior

- Phylogeny (Evolution) – How does this behavior arise in the species? How did the behavior evolve over generations?

- Adaptive Value (Function) – Why is the behavior adaptive for the species? How does this function contribute to survival and reproduction?

One example is related to bird song; how and why do birds sing. What mechanisms underlie song production (i.e., neural, sensory, hormonal, and motor systems)? How is the song acquired and modified throughout the lifespan of the bird? What are the differences in the acoustics across a comparison of species? How does the bird song play a role in defending a territory or in reproductive success?

Another example would examine the behavior of social grooming (e.g., allogrooming) in non-human primates. What triggers allogrooming behavior? What age does allogrooming begin and which animals engage in the behavior? Does this development change depend on the environmental habitat or the type of social group? Within the comparison of different social groups, when might it change from hygienic function to a social function? Is allogrooming used to increase social bonding and health and/or reduce tension in the social hierarchy?

Tinbergen's contributions expanded the understanding of behavior in a variety of species such as black-headed gulls, graylag geese, herring gulls, stickleback fish, and digger's wasps. In each of the studies, he created systematic observations and experiments to investigate animal behavior.

## Black-Headed Gulls

Black-headed gulls naturally take empty egg shells and drop or relocate them some distance from the nest. During this time the chicks are left alone in their nest. Why do black-headed gulls remove broken eggshells from the nest after the chick hatch? This is an example of an ultimate question. Tinbergen examined why the chicks would be left vulnerable by this behavior. He found through experimental studies that the



function was to decrease the predation of their offspring which was the results of an adaptive mechanism (Tinbergen et al. 1962). Tinbergen also explored how the stimuli (i.e., egg) could alter the type of behavior that the gull exhibited. He manipulated a model egg in various ways such as the color, shape, size, and distance from the nest. In doing so he measured the frequency and latency of the specific behavior that the gull was engaged in (e.g., rolling vs carrying).

### **Graylag Goose**

Tinbergen also worked with Lorenz on graylag geese and their stereotypical egg rolling behavior (Lorenz and Tinbergen 1939, 1970). An automatic response of the goose exists when an egg is located outside of the nest. The automatic response of rolling the egg back into the nest was discovered to be a complex instinctive behavior. If the egg was removed during the recovery response, the goose would continue with the complex response. This is when Tinbergen and Lorenz further examined this by using a variety of egg-shaped stimuli to discover that geese continued the “fixed action pattern” regardless of if the egg was removed. This fixed action pattern was the result of exposure to a specific sensory stimulus (i.e., sign stimulus) which created an innate sequence of reflexive responses. In the study the geese were also provided multiple varieties of “eggs” outside of the nest in which the size, pattern, shape, and color were modified. Through this investigation they determined there was a preferred egg but it was not the normal egg. The artificial egg they preferred was larger, had a more complex speckled pattern, and was darker in the green color. These unrealistic cues were labeled as “supernormal stimuli.”

### **Herring Gull Chicks**

Another one of Tinbergen’s classic studies examined herring gulls (Tinbergen and Perdeck 1950;

Tinbergen 1960). Herring gull chicks display an automatic pecking behavior to a red spot located on the mother’s beak. The mother’s beak then produces an automatic response of regurgitation. In the classic experiments, Tinbergen explored how a “model,” the position of the red spot (distance above the ground), and alternated response time could influence the pecking behavior of the chicks. He found that the location sign stimulus (i.e., the red spot) on the model played a role in the automatic response of the chick. When the red spot was toward the bottom and end of the beak, the chicks were more likely to peck. Tinbergen also explored how a narrow boldly colored vertical stick with horizontal movement would be perceived by the chicks. He found by intensifying the color and the contrast the model became a supernormal stimulus which elicited a supernormal response. The red stick shape and contrast created more pecking than to a real beak.

### **Stickleback Fish**

Tinbergen also explored this topic by examining how sign stimuli could control aggressive and sexual behavior of stickleback fish. During breeding season males displayed the fixed action pattern, which changed the color of their “belly” to red. Due to the competition of territory of the males, the color red appears to be the stimulus that triggers the notable difference in territory. If another red-bellied fish, male or female, came into their territory, it created an aggressive response. Tinbergen explored what aspect of the other fish created the automatic response and discovered it was the color red (Tinbergen 1951). This indicated that it did not have to be just a fish that had the color red on it but any object with the sign stimulus (i.e. color red) in the experiment created the fixed action pattern. In relation to courtship behavior, Tinbergen found that a swollen “belly” of a model fish, in addition to the posture, stimulated the “zigzag dance” of the male. Throughout the study it was indicated that there were multiple sign stimuli that were used in the sequence of the

reproduction. During the building of the egg tunnel, by the male, is when the red belly indicated territorial aggressive behavior. However, after the egg tunnel has been completed, a female approached and became the trigger or the sign stimulus (i.e., the swollen abdomen of the female). The swollen abdomen creates the zigzag dance of the male. The female is then stimulated by the red belly of the male. In this case the size of the abdomen of the female will draw the attention and response of the male, and the red belly of the male will draw in the female to the egg tunnel. Tinbergen examined this process using a variety of models throughout this process.

### Digger Wasps: It Relates to the Landmark Use to Lay Eggs

Tinbergen also examined the homing behavior in digger wasps, specifically the use of landmarks (Tinbergen and Kruyt 1972). How do digger wasps find their homes among a variety of nests in a location?

This is a proximate question. Digger wasps lay eggs in a burrow, for predator avoidance, after which they exit the burrow and fly around to possibly locate landmarks to assist in finding the burrow. Tinbergen first explored this aspect by creating a circle of pinecones around the entrance to the burrow. When the wasp was out foraging, they relocated the circle of pine cones. They found that the returning wasp went to the location where the pinecones were relocated. Tinbergen also explored if scents, type of object, or arrangement of the landmarks provided the burrow location. Through his studies he found that scent and the type of object were not used to locate the burrows. However, when the arrangement of the landmarks was examined, it was found that this did contribute to the landmarking principle. For example, when the wasp left the burrow, it had a circular arrangement of pinecones. Once the wasp left, a triangle of pinecones were put above the burrow and a circular arrangement of rocks were placed to the side of the burrow. When the wasp returned, it traveled to the circular arrangement of the rocks.

Tinbergen's research on patterns of behavior played a role in the development of ethology, the confirmation of field research, and the development of modern behavioral ecology. Tinbergen also contributed the connection between comparative psychologists and European ethologists. His classical studies are currently involved not only in biology but also in the field of psychology. He was not only a professor and researcher; he also became a writer and filmmaker. In addition to his research contribution, he also provided interest and concern in diplomacy, goodwill, and humanity.

### Cross-References

- ▶ [Aggression](#)
- ▶ [Allogrooming](#)
- ▶ [Autism](#)
- ▶ [Ethology](#)
- ▶ [Fixed Action Patterns](#)
- ▶ [Innate Releasing Mechanism](#)
- ▶ [Karl Von Frish](#)
- ▶ [Konrad Lorenz](#)
- ▶ [Ontogeny](#)
- ▶ [Orientation](#)
- ▶ [Phylogeny](#)
- ▶ [Proximate Mechanism](#)
- ▶ [Sign Stimulus](#)
- ▶ [Zoology](#)

### References

- Burkhardt, R. W., Jr. (2005). *Patterns of behavior: Konrad Lorenz, Niko Tinbergen, and the founding of ethology*. Chicago: University of Chicago Press.
- Kruuk, H. (2003). *Niko's nature: A life of Niko Tinbergen and his science of animal behaviour*. Oxford: Oxford University Press.
- Lorenz, K., & Tinbergen, N. (1939). Taxis und Instinkthandlung in der Eirollbewegung der Graugans. I. *Ethology*, 2(1-3), 1-29.
- Lorenz, K., & Tinbergen, N. (1970). Taxis and instinctive behaviour pattern in egg-rolling by the Greylag goose. In *Studies in animal and human behavior* (Vol. 1). Cambridge, MA: Harvard University Press.
- Shettleworth, S. J. (2010). *Cognition, evolution, and behavior*. Oxford University Press.

- Tinbergen, N. (1951). *The study of instinct*. Oxford: Clarendon Press.
- Tinbergen, N. (1953). *The herring gull's world*. London: Collins.
- Tinbergen, N. (1958). *Curious naturalists*. London: Country Life.
- Tinbergen, N. (1960). Comparative studies of the behaviour of gulls (Laridae): A progress report. *Behaviour*, 15 (1), 1–69.
- Tinbergen, N. (1963). On aims and methods of ethology. *Ethology*, 20(4), 410–433.
- Tinbergen, N. (1972). *The animal in its world* (Vol. 1). London: Allen & Unwin/Harvard University Press.
- Tinbergen, N. (1973a). Nikolaas Tinbergen – Biographical. Retrieved from [https://www.nobelprize.org/nobel\\_prizes/medicine/laureates/1973/tinbergen-bio.html](https://www.nobelprize.org/nobel_prizes/medicine/laureates/1973/tinbergen-bio.html)
- Tinbergen, N. (1973b). *The animal in its world* (Vol. 2). London: Allen & Unwin/Harvard University Press.
- Tinbergen, N., & Kruyt, W. (1972). On the orientation of the digger wasp, *Philanthus triangulum* Fabr. III. Selective learning of landmarks. In N. Tinbergen (Ed.), *The animal and its world*. Cambridge, MA: Harvard University Press. (Originally published in 1938).
- Tinbergen, N., & Perdeck, A. C. (1950). On the stimulus situation releasing the begging response in the newly hatched herring gull chick (*Larus argentatus argentatus* Pont.) *Behaviour*, 3(1), 1–39.
- Tinbergen, N., & Tinbergen, E. A. (1972). *Early childhood autism – An ethological approach*. Berlin: Parey.
- Tinbergen, N., Broekuyzen, G. J., Feekes, F., Houghton, J. C. W., Kruuk, H., & Szulc, E. (1962). Egg shell removal by the black headed gull, *Larus ridibundus* L.: A behaviour component of camouflage. *Behaviour*, 19(1–2), 74–117.

# S

## Stand and Wait Feeding Behavior

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### Synonyms

[Stand and wait foraging behavior](#); [Stand-and-wait feeding](#)

### Definition

Stand and wait feeding behavior is a strategy utilized by avian predators that stand still in water or on land and wait for prey to approach.

### Introduction

Stand and wait feeding behavior is a common strategy employed by foraging wading birds and is particularly common in visual feeders such as herons (Kushlan 1978a; Meyerriecks 1960). It is characterized by different standing postures and neck positions, but in all cases the predator stands while waiting for prey to approach.

## Description of Behavior

Stand and wait feeding is one of the most common foraging strategies employed by wading birds (Meyerriecks 1960). Typically, foraging predators stand motionless on land, at the edge of a body of water, or in shallow water. When prey approaches within range, the predator strikes rapidly, either seizing the prey or impaling it on its bill. Prey is often swallowed whole. Large prey may be stunned or killed before swallowing, while smaller items are often swallowed live. Strikes (successful or not) are often followed by dipping the bill into the water and then shaking the head.

Because stand and wait feeding behavior is common across a variety of species, it is associated with a diversity of postures and neck positions (Kushlan 1978a). Wading bird posture ranges from a hunched or crouched position to full upright position, with intermediate variations of upright posture in between these two extremes. Similarly, neck posture can result in a head that is retracted or fully extended, or any variation in between. Oftentimes the bill faces the water with the wader peering down, while other times the head is cocked or both the head and neck are tilted (Kushlan 1978a). Head tilting or cocking may be used to reduce glare from the sun (Kushlan 1978a). In addition to the variation in positions and postures, there are also a number of slight variations to stand and wait feeding. For example, stand and wait predators can bait prey while they are waiting by placing a piece of food in the water

to attract prey (Lovell 1958). Head or neck swaying are also common additions to stand and wait feeding (Meyerriecks 1962). Stand and wait feeding behavior can be interchanged with other feeding behaviors, including slowly wading or walking.

Stand and wait foraging is associated with adaptations that may facilitate feeding in a variety of habitats and throughout the day. For example, neck anatomy allows stand and wait foragers to extend the neck rapidly while thrusting for prey. Water depth is an important determinant of prey availability to foraging waders (Gawlik 2002), with foraging wading birds that feed by standing in water restricted by leg length (Kushlan 1976; Powell 1987). Shallow water is generally preferred (Gawlik 2002). Wading birds with shorter legs may also stand on the water edge or perch, for example on logs, rocks or roots. Additionally, wading birds that feed using this strategy often have either white or dark plumage, and it has been hypothesized that either color type can be adaptive towards reducing conspicuousness to prey (Kushlan 1978a). Specifically, white foraging birds may be less visible from below during the day, and birds with dark plumage may be less visible from below at night or when foraging in shadows (Kushlan 1978a). Specialized optics allow foraging wading birds to feed using the stand and wait strategy during the day and at night.

Stand and wait feeding is a common strategy whether foraging solitarily or in groups. Additionally, it is common both in natural habitats (e.g., wetlands, tidal areas) and anthropogenic habitats such as flooded rice fields (Elphick 2000) or canals.

## Conclusion

Stand and wait feeding is one of the most common foraging strategies employed by wading birds. As

the name suggests, birds stand “frozen” while feeding, which is in direct contrast to active feeding. This can conserve energy, making stand-and-wait feeding a useful strategy to maximize energy intake (Kushlan 1978b). Resource partitioning based on foraging adaptations, including leg length and temporal feeding strategies, may help to reduce competition among wading birds and to structure wading bird communities.

## Cross-References

- ▶ [Aves \(Birds\)](#)
- ▶ [Central-Place Foraging](#)
- ▶ [Foraging](#)
- ▶ [Optimal Foraging Theory](#)

## References

- Elphick, C. S. (2000). Functional equivalency between rice fields and seminatural wetland habitats. *Conservation Biology*, 14(1), 181–191.
- Gawlik, D. E. (2002). The effects of prey availability on the numerical response of wading birds. *Ecological Monographs*, 72(3), 329–346.
- Kushlan, J. A. (1976). Feeding behavior of North American herons. *Auk*, 93(1), 86–94.
- Kushlan, J. A. (1978a). Feeding ecology of wading birds. In A. J. Sprunt, J. C. Ogden, & S. Winckler (Eds.), *Wading birds* (pp. 249–297). New York: National Audubon Society.
- Kushlan, J. A. (1978b). Nonrigorous foraging by robbing egrets. *Ecology*, 59(4), 649–653.
- Lovell, H. B. (1958). Baiting of fish by a Green heron. *Wilson Bulletin*, 70, 280–281.
- Meyerriecks, A. J. (1960). Comparative breeding behavior of four species of North American herons. *Publications of the Nuttall Ornithological Club*, 2, 1–158.
- Meyerriecks, A. J. (1962). Diversity typifies heron feeding. *Natural History*, 71, 48–59.
- Powell, G. V. N. (1987). Habitat use by wading birds in a subtropical estuary: Implications of hydrography. *Auk*, 104, 740–749.

# G

## Geometric Encoding

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### Synonyms

[Global geometry](#); [Local geometry](#); [Spatial reorientation](#)

Successful movement between locations first requires the determination of a direction of travel, and understanding the process of determining a direction is the central focus of orientation research. As shown in the top panel of Fig. 1, the general approach to understanding orientation involves training disoriented participants to respond to a particular location within a rectangular enclosure (left). Importantly, this location is often uniquely specified by a distinctive feature. Interestingly, tests in the absence of the distinctive features reveal that participants not only respond to the originally trained location but also to its 180° rotationally equivalent location (right). Responses to this 180° rotationally equivalent location are termed a *rotational error* (for a review, see Cheng et al. 2013).

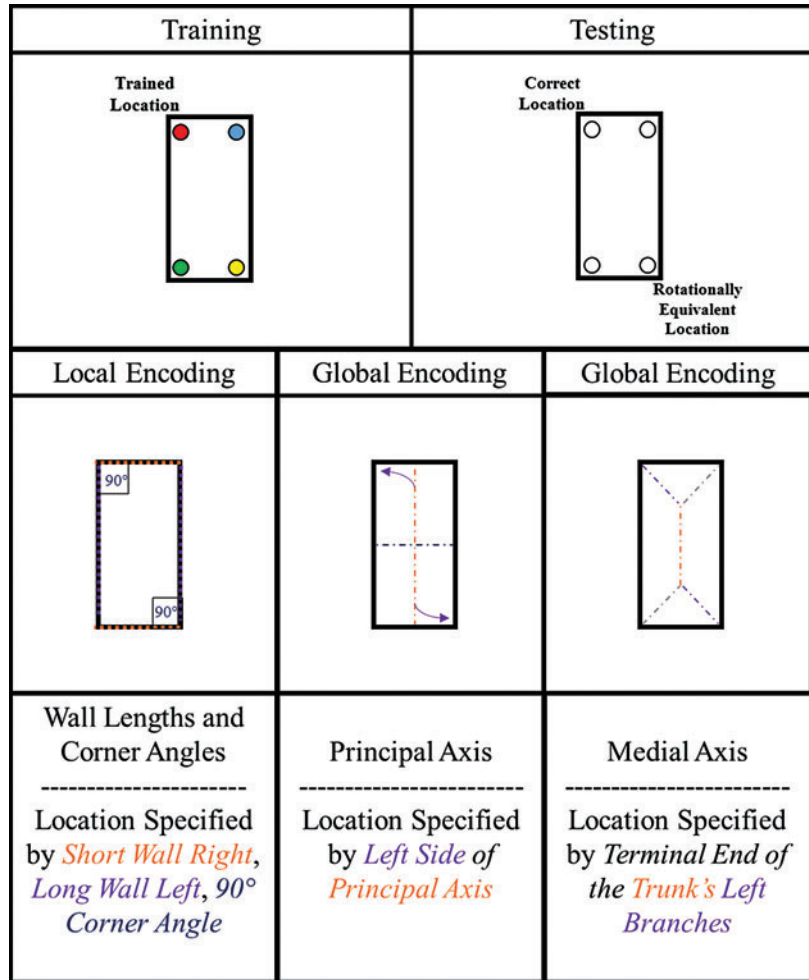
The occurrence of the rotational error is particularly interesting because it suggests that participants learn something about the geometric shape of the enclosure itself during training, and such

learning about the geometric shape of the enclosure during training is unneeded because it is neither necessary nor sufficient to determine the correct location (for a review, see Cheng et al. 2013). Specifically, the correct location is uniquely and sufficiently specified by the distinctive feature; yet in its absence, participants respond as if they learned the correct location with respect to the environmental shape, and the rotational error is suggested to occur because, in the absence of the distinctive feature, environmental geometry alone cannot disambiguate the correct from the rotationally equivalent location.

The occurrence of the rotational error has been observed in ants, chicks, pigeons, fish, and primates – including human children and human adults (for a review, see Cheng et al. 2013). In human adults, the rotational error also occurs in a sensory modality other than vision (Sturz et al. 2014). Specifically, blindfolded adults trained to respond to a particular corner of a rectangle designated by a unique texture respond to the trained and rotationally equivalent locations when the unique texture is absent. This occurrence across species and sensory modalities suggests that orientation via geometric cues may be a ubiquitous and fundamental process in the animal kingdom (see Tommasi et al. 2012). As a result, determining the nature of this geometric encoding – environmental points, lines, angles, and overall shape to determine a direction – has received considerable research attention (see Sutton 2009), and manipulations of shape from training



**Geometric Encoding, Fig. 1** *Top Panels.* Illustration of the Training and Testing components of the reorientation paradigm. *Bottom Panels.* Illustration of local and global geometric encoding strategies



to testing have revealed two basic categories of geometric cues used during reorientation: *local geometric cues* and *global geometric cues* (see Bodily et al. 2011; Lubyk et al. 2012; Sturz et al. 2012; for a review, see Sutton 2009). Both types of cues explain the presence of the rotational error but differ with respect to what is encoded about environmental geometry.

As shown in Fig. 1 (bottom left), local geometric cues are independent cues such as wall lengths and corner angles that constitute the environmental shape (see Miller and Shettleworth 2007). Thus, local geometric encoding would involve encoding the correct location during training as a location specified by short wall right, long wall left, and 90° corner angle. Such local geometric encoding during training explains the occurrence

of the rotational error during testing because both the correct and rotationally equivalent locations are located at the right side of a short wall, the left side of a long wall, and at a 90° corner angle. In contrast, global geometric cues (often derived from computational geometry) are dependent on the overall shape of the environment because they must be encoded from the overall shape of the environment (see Sturz and Bodily 2012). For example, the principal axis of space, which runs through the centroid and approximate length of the space is a summary parameter derived from the boundaries (see Sturz et al. 2011). Thus, global geometric coding with respect to the principal axis would involve encoding the correct location during training as the location specified by the left side of the principal axis. Such global geometric

encoding during training explains the occurrence of the rotational error during testing because both the correct and rotationally equivalent locations are located at the left side of the principal axis. Similarly, the medial axis of space which is a trunk and branch system that captures overall shape information is also derived from the boundaries (see Kelly et al. 2011). Thus, global geometric encoding with respect to the medial axis of space would involve encoding the correct location during training as the location specified by the terminal end of the trunk's left branch. Such global geometric encoding during training explains the occurrence of the rotational error during testing because both the correct and rotationally equivalent locations are located at the terminal end of the trunk's left branch.

Despite recent debate about which global geometric cue may be encoded (see Sturz and Bodily 2012), it is clear that both local and global geometric cues are encoded and used for orientation (see Cheng et al. 2013). As importantly, it is also clear that a sense component (i.e., left or right) is part of this encoding process (see Sovrano and Vallortigara 2006). Current research is continuing to manipulate aspects of the environment from training to testing to further illuminate the geometric cues used to reorient with respect to the environment.

## Cross-References

- ▶ [Cognitive Map](#)
- ▶ [Encoding](#)
- ▶ [Geometric Module](#)
- ▶ [Landmark](#)
- ▶ [Navigation](#)
- ▶ [Orientation](#)
- ▶ [Orienting](#)
- ▶ [Place Versus Response Learning](#)
- ▶ [Spatial Memory](#)
- ▶ [Spatial Relations](#)

## References

- Bodily, K. D., Eastman, C. K., & Sturz, B. R. (2011). Neither by global nor local cues alone: Evidence for a unified orientation process. *Animal Cognition*, *14*, 665–674.
- Cheng, K., Huttenlocher, J., & Newcombe, N. S. (2013). 25 years of research on the use of geometry in spatial reorientation: A current theoretical perspective. *Psychonomic Bulletin & Review*, *20*, 1033–1054.
- Kelly, D. M., Chiandetti, C., & Vallortigara, G. (2011). Re-orienting in space: Do animals use global or local geometry strategies? *Biology Letters*, *7*, 372–375.
- Lubyk, D. M., Dupuis, B., Gutiérrez, L., & Spetch, M. L. (2012). Geometric orientation by humans: Angles weigh in. *Psychonomic Bulletin & Review*, *19*, 436–442.
- Miller, N. Y., & Shettleworth, S. J. (2007). Learning about environmental geometry: An associative model. *Journal of Experimental Psychology: Animal Behavior Processes*, *33*, 191–212.
- Sovrano, V. A., & Vallortigara, G. (2006). Dissecting the geometric module: The association of metric and landmark information with sense in animals' spatial reorientation. *Psychological Science*, *17*, 616–621.
- Sturz, B. R., & Bodily, K. D. (2012). On discriminating between geometric strategies of surface-based orientation. *Frontiers in Psychology*, *3*, 112. doi:10.3389/fpsyg.2012.00112.
- Sturz, B. R., Gurley, T., & Bodily, K. D. (2011). Orientation in trapezoid-shaped enclosures: Implications for theoretical accounts of geometry learning. *Journal of Experimental Psychology: Animal Behavior Processes*, *37*, 246–253.
- Sturz, B. R., Forloines, M. R., & Bodily, K. D. (2012). Enclosure size and the use of local and global geometric cues for reorientation. *Psychonomic Bulletin & Review*, *19*, 270–276.
- Sturz, B. R., Gaskin, K. A., & Roberts, J. E. (2014). Incidental encoding of enclosure geometry does not require visual input: Evidence from blind-folded adults. *Memory & Cognition*, *42*, 935–942.
- Sutton, J. E. (2009). What is geometric information and how do animals use it? *Behavioural Processes*, *80*, 339–343.
- Tommasi, L., Chiandetti, C., Pecchia, T., Sovrano, V. A., & Vallortigara, G. (2012). From natural geometry to spatial cognition. *Neuroscience and Biobehavioral Reviews*, *36*, 799–824.

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# A

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## Andrew Whiten

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### Biography

Andrew (Andy) Whiten is Emeritus Wardlaw Professor at the School of Psychology and Neuroscience, University of St Andrews, Scotland. He is an elected Fellow of the British Academy, the Royal Society of Edinburgh, and the International Cognitive Science Society. Whiten's research focuses on social learning and cultural transmission, providing insights into this "second inheritance system" and the role it plays in shaping behavior in concert with genetic inheritance and individual learning. Through his collaborations, Whiten has published papers on humans and non-human primates and has used experimental and observational techniques to answer questions about the social drivers of primate cognition.

Whiten joined the University of St Andrews as a Lecturer in 1975 after studying at the Universities of Sheffield, Bristol, and Oxford. He became Professor of Evolutionary and Developmental Psychology at the University of St Andrews in 1997 and was made Wardlaw Professor in 2001. In 2003, Whiten founded the Center for Social Learning and Cognitive Evolution and 5 years

later established the Living Links to Human Evolution primate research center, housed at Edinburgh Zoo, providing a forum for public engagement with science in a zoo setting.

### Behavioral Ecology of Baboons

Whiten's early research focused on the behavioral ecology of chacma baboons (*Papio ursinus*) living in the Drakensberg mountains of South Africa and, later, olive baboons (*P. anubis*) in Kenya. This field research was conducted in collaboration with Richard Byrne, Peter Henzi, and Robert Barton.

### Machiavellian Intelligence

Initially inspired by their observations of "tactical deception" in wild baboons, in their 1988 book *Machiavellian Intelligence*, Andy Whiten and Richard Byrne highlighted links between the various aspects of primate intelligence in the social domain (Byrne and Whiten 1998). Framed against the earlier work of Nicholas Humphrey and Alison Jolly, Byrne and Whiten curated a volume of both new and previously published chapters that provided support for the "social intelligence hypothesis." Thirty years on, the ideas put forward in *Machiavellian Intelligence* still resonate and continue to be investigated in contemporary studies of primate cognition and behavior.

## Chimpanzee Culture

In the 1990s, Whiten led a consortium of primatologists to publish a report on chimpanzee behavior studied at long-term field sites across Africa (Whiten et al. 1999). In this seminal article, the authors compared the behavioral repertoires of chimpanzees living in seven different communities: Bossou (Guinea), Taï Forest (Ivory Coast), Gombe (Tanzania), Mahale M-group (Tanzania), Mahale K-group (Tanzania), Kibale Forest (Uganda), and Budongo Forest (Uganda). Through this collaborative effort, the authors identified 39 behaviors that were observed to be performed by chimpanzees in certain communities but not others. The authors proposed that the variance in behavioral patterns could be “seen to resemble those in human societies, in which differences between cultures are constituted by a multiplicity of variations in technology and social customs” (Whiten et al. 1999, p. 685), an idea that they crystallized as *Cultures in Chimpanzees*. This collaborative endeavor was expanded to include two additional sites (Lopé, in Gabon, and Assirik, in Senegal), and in a follow-up paper, the authors reviewed chimpanzee behaviors that were universal and others for which an environmental cause could be attributed, in addition to possible socially learned cultural behaviors (Whiten et al. 2001). When they published their original paper, Whiten et al. (1999) recognized that behavioral traditions might not be unique to chimpanzees and such traditions have since been reported for a variety of other primate species, including orangutans, capuchin monkeys, and spider monkeys, as well as nonprimate animal species. While *Machiavelian Intelligence* called researchers to question behavioral theories of technical intelligence and instead to consider social influences on cognitive evolution, *Cultures in Chimpanzees* (Whiten et al. 1999) called us to question the uniqueness of human culture and the potential power of social learning in shaping animal behavior.

## Experimental Methods for Studying Social Learning

To gain a deeper understanding of the social and cognitive mechanisms that underlie primate social learning, Whiten has conducted numerous experimental studies with wild and captive nonhuman primate populations and also with human participants. Much of this research has incorporated a two-action task that can be solved in one of two arbitrary ways. The use of a two-action task allows the researcher to determine both if the naïve subject can learn a solution from observing an expert and also if they use the same method as the expert to do so. To increase the ecological validity of such tests, Whiten created tasks designed to mimic the actions required by wild primates to remove the tough casings of wild fruits or to obtain foods like honey or insects via extractive foraging techniques (Whiten et al. 1996). These tasks, dubbed “artificial fruits,” have ranged in their design and complexity, allowing researchers to test the fidelity of social learning (e.g., imitation versus emulation); hierarchical and serial imitation, and the ability of primates to make and use tools to extract food from these devices.

Whiten employed one such two-action task (the “pan-pipes”) in a groundbreaking study of captive chimpanzee social learning of tool use, run in collaboration with Victoria Horner and Frans de Waal (Whiten et al. 2005). Rather than simply testing the transmission of information between two individuals as previous social learning tests had done, Whiten et al. (2005) exposed two entire groups of chimpanzees to a trained chimpanzee model in an “open diffusion” test design. Not only did this study show that the majority of observer chimpanzees were able to learn the task from observing the trained model, but also that they predominantly matched the specific method used by the model. Thus, the newly introduced behavior spread throughout each of the two social groups tested, mimicking culturally transmitted behavioral variation reported for wild chimpanzee communities (Whiten et al. 1999). Furthermore, the findings from this study challenged previous assumptions about primate

social learning (i.e., it was restricted to enculturated individuals raised in human-centric environments or that social learning could only occur during the juvenile years). This open diffusion technique has subsequently been applied to study social learning in other nonhuman primate species and with human children. It has also been adapted to ask more nuanced questions about how, what, and when information is transmitted among primates (Kendal et al. 2015).

Whiten and colleagues have also run “diffusion chain” experiments, akin to the “telephone game,” that mimic vertical transmission down generations. This method provides more experimental control over what information is transmitted, as well as who has the opportunity to learn from whom. Whiten has applied this to chimpanzees, orangutans, and human children, revealing high-fidelity transmission of behavioral foraging techniques.

### **Diversity in Studies of Social Cognition in Captive Primate Populations**

The majority of Whiten’s research with captive primates has focused on social cognition, with an emphasis on social learning. His work with captive primates has encompassed a broad phylogenetic perspective, with studies being run with chimpanzees (*Pan troglodytes*), gorillas (*Gorilla gorilla gorilla*), orangutans (*Pongo abelii* and *P. pygmaeus*), capuchin monkeys (*Cebus apella*), squirrel monkeys (*Saimiri sciureus*), and marmoset monkeys (*Callithrix jacchus*). This research has been run at a variety of facilities including sanctuaries (e.g., Ngamba Island Chimpanzee Sanctuary, Uganda), zoos (e.g., Zoo Atlanta, USA, and Edinburgh Zoo, UK), and laboratories (e.g., Yerkes National Primate Research Center, USA, and UT MD Anderson Cancer Center, USA). Beyond confirming the social diffusion of behaviors (Whiten et al. 2005), Whiten’s work has attempted to tease apart social learning strategies (“who” do primates copy, e.g., Kendal et al., 2015) and mechanisms (“what” do primates copy, e.g., Hopper et al. 2015), as well as the

social and environmental conditions that best support social learning (Caldwell and Whiten 2003).

### **Studies with Wild Primate Populations**

In recent years, Whiten has expanded his experimental studies of primate social learning to include field research, returning to South Africa, but now to study vervet monkeys (*Chlorocebus aethiops*). Working in collaboration with Erica van de Waal at her field site, as part of the Inkawu Vervet Project, Whiten has been involved in a number of field experiments on social learning (e.g., van de Waal et al. 2013). Through the use of artificial fruit tasks and the provision of novel foods, van de Waal, Whiten, and colleagues have revealed when and how information is transmitted among monkeys within a troop, as well as shedding light on how monkeys weigh their own personal experience against social information when they emigrate to a new group. These field experiments either reflect or have stimulated “sister” studies run with captive primates, allowing comparison between captivity and the field, as well as across species (e.g., Vale et al. 2017).

### **Studies with Human Children**

From early times Whiten’s experimental work investigating primate social learning was comparative, including both human and nonhuman primate subjects (Whiten et al. 1996). He has continued to provide a comparative perspective throughout his career. Just as with nonhuman primates, Whiten has tested human children with artificial fruit analogs, in dyadic, diffusion chain, and even open diffusion paradigms (Whiten and Flynn 2010). His work has revealed both the similarities and differences in how we learn new skills compared to our nonhuman cousins and has expanded to include work focused on other areas of social cognition (e.g., prosociality, Claidière et al. 2015). To better understand the relationship between children’s theory of mind understanding and their capacity to learn from others, Whiten has

also investigated the social learning capacities of children with autism (e.g., Williams et al. 2001).

## Public Engagement with Science

In addition to conducting research, Whiten has demonstrated an extensive commitment to public engagement with science, particularly evident in the design of the Living Links to Human Evolution research center at Edinburgh Zoo, of which Whiten was a founding director. At Living Links, visitors to the zoo can observe scientists running behavioral and cognitive research within two mixed-species communities of capuchins and squirrel monkeys. The dedication Whiten has shown to public understanding of science was recognized by the Royal Society of Edinburgh, who awarded him their Senior Prize and Medal for Public Engagement in 2014.

## Legacy

Whiten's impact on the field of comparative psychology, particularly on the study of primate social cognition, is far reaching. Both through his own research and that of his collaborators and former students, Whiten's theories and research findings continue to influence the field. His legacy is recognized both through the continued relevance of his work and also through the awards he has received throughout his career that include the Osman Hill Medal, awarded by Primate Society of Great Britain in 2010, the Sir James Black Medal, awarded by the Royal Society of Edinburgh in 2013, and from honorary degrees bestowed by Heriot Watt University (2015), the University of Stirling (2016), and the University of Edinburgh (2017).

## Cross-References

- ▶ [Affordance Learning](#)
- ▶ [Bennett G. Galef](#)
- ▶ [Bill McGrew](#)
- ▶ [Comparative Psychology](#)

- ▶ [Co-operation](#)
- ▶ [Copying](#)
- ▶ [Cultural Assemblage](#)
- ▶ [Cultural Transmission](#)
- ▶ [Culture](#)
- ▶ [Cumulative Culture](#)
- ▶ [Deferred Imitation](#)
- ▶ [Diffusion](#)
- ▶ [Do-as-I-do Experiments](#)
- ▶ [Emulation](#)
- ▶ [Frans de Waal](#)
- ▶ [Ghost Control](#)
- ▶ [Goal-directed Behavior](#)
- ▶ [Imitation](#)
- ▶ [Learning](#)
- ▶ [Local Enhancement](#)
- ▶ [Machiavellian Intelligence](#)
- ▶ [Mimicry](#)
- ▶ [Non-human Primates](#)
- ▶ [Primate Cognition](#)
- ▶ [Primates](#)
- ▶ [Problem-solving](#)
- ▶ [Rational Imitation](#)
- ▶ [Richard Byrne](#)
- ▶ [Social Learning](#)
- ▶ [Theory of Mind](#)
- ▶ [Trab-tube Problem](#)

## References

- Byrne, R., & Whiten, A. (1998). *Machiavellian intelligence: Social expertise and the evolution of intellect in monkeys, apes, and humans*. Oxford: Oxford University Press.
- Caldwell, C. A., & Whiten, A. (2003). Scrounging facilitates social learning in common marmosets, *Callithrix jacchus*. *Animal Behaviour*, 65(6), 1085–1092.
- Claidière, N., Whiten, A., Mareno, M. C., Messer, E. J. M., Brosnan, S. F., Hopper, L. M., Lambeth, S. P., Schapiro, S. J., & McGuigan, N. (2015). Selective and contagious prosocial resource donation in capuchin monkeys, chimpanzees and humans. *Scientific Reports*, 5, 7631.
- Hopper, L. M., Lambeth, S. P., Schapiro, S. J., & Whiten, A. (2015). The importance of witnessed agency in chimpanzee social learning of tool use. *Behavioural Processes*, 112, 120–129.
- Kendal, R., Hopper, L. M., Whiten, A., Brosnan, S. F., Lambeth, S. P., Schapiro, S. J., & Hoppitt, W. (2015). Chimpanzees copy dominant and knowledgeable



- individuals: Implications for cultural diversity. *Evolution and Human Behavior*, 36(1), 65–72.
- Vale, G. L., Davis, S. J., van de Waal, E., Schapiro, S. J., Lambeth, S. P., & Whiten, A. (2017). Lack of conformity to new local dietary preferences in migrating captive chimpanzees. *Animal Behaviour*, 124, 135–144.
- van de Waal, E., Borgeaud, C., & Whiten, A. (2013). Potent social learning and conformity shape a wild primate's foraging decisions. *Science*, 340(6131), 483–485.
- Whiten, A., & Flynn, E. (2010). The transmission and evolution experimental microcultures in groups of young children. *Developmental Psychology*, 46(6), 1694–1709.
- Whiten, A., Custance, D. M., Gomez, J. C., Teixidor, P., & Bard, K. A. (1996). Imitative learning of artificial fruit processing in children (*Homo sapiens*) and chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, 110(1), 3–14.
- Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R. W., & Boesch, C. (1999). Cultures in chimpanzees. *Nature*, 399, 682–685.
- Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R. W., & Boesch, C. (2001). Charting cultural variation in chimpanzees. *Behaviour*, 138(11–12), 1481–1516.
- Whiten, A., Horner, V., & de Waal, F. B. M. (2005). Conformity to cultural norms of tool use in chimpanzees. *Nature*, 437, 737–740.
- Williams, J. H., Whiten, A., Suddendorf, T., & Perrett, D. I. (2001). Imitation, mirror neurons and autism. *Neuroscience and Biobehavioral Reviews*, 25(4), 287–295.

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## Ludwig Huber

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### Personal History and Overview of Research

Ludwig Huber was born in Neunkirchen, Lower Austria, on 25 July 1964, but raised in Tarnitz. He attended Sachsenbrunn, a classical grammar school near Kirchberg/Wechsel for 8 years, where he was educated in traditional humanistic studies, including Latin and ancient Greek. Despite this catholic-humanistic education, Huber nourished interest in biology from an early age. As a child he dreamed of becoming a biologist, mainly due to his fascination with African fauna (actually by watching TV documentaries and reading books about the work of Jane Goodall, Diane Fossey, and Bernhard Grzimek). Shortly before starting his biology studies at the University of Vienna, he participated in a symposium celebrating the 80th birthday of Konrad Lorenz in Laxenburg (south of Vienna). It was here that he got his first hands-on lessons in ethology from well-known scholars of Lorenz, including Bernhard Hassenstein, Sverre Sjölander, Wolfgang Schleidt, Iräneus Eibl-Eibesfeldt, and Antal Festetics. Still, he was most fascinated by

Rupert Riedl, a professor of theoretical biology at the University of Vienna, who was not a scholar but a companion of Lorenz in his later years. His speech drew Huber's attention away from classical ethology and toward evolutionary and cognitive biology.

During Huber's biology studies (major, zoology; minor, philosophy and philosophy of science) at the University of Vienna (1983–1988), he broadened and deepened his interests with a focus first on comparative morphology (homology) and later on evolutionary theory (the debates about group selection, exaptation, and constraints). His latent interest in behavioral biology was nourished by an excursion to the Maldives, where he compared different foraging strategies of coral reef fish. Nevertheless, he was taken by Rupert Riedl's lectures and seminars on evolutionary epistemology, the most interesting of which being dedicated to an interdisciplinary inquiry into the theoretical foundations of biology. This motivated him to study the philosophy of science (Erhard Oeser) as an accessory discipline with a focus on the Viennese strand of evolutionary epistemology following Ernst Mach, Ludwig Boltzmann, and Karl Popper. Still, the major influence on his later career arose from writings of Konrad Lorenz and Rupert Riedl, most notably the books "Behind the Mirror" and "Biology of Knowledge," and two conferences on evolutionary epistemology, organized by Rupert Riedl at the University of Vienna, with Karl Popper and Konrad Lorenz as keynote speakers.

Shortly after these influential events, Huber started his diploma thesis project, which examined the power of associative learning as a means of anticipating events that do not follow alternation sequences. Indeed goldfish (*Carassius auratus*) proved able to adapt to a complex sequence of reinforced and non-reinforced events. This study was part of Rupert Riedl's larger project dedicated to applied questions of evolutionary epistemology, namely, the parallel working of rational and irrational (called "ratiomorphic") processes in human thinking. Inspired by vivid discussions during two visits of Konrad Lorenz in autumn 1988, Riedl and Huber tested several populations of humans, varying in age and education, on how they distinguish between foreseeable and unforeseeable event series. Surprisingly, with the exception of mathematicians, most participants relied on the "negative recency effect," also known as the "gambler's fallacy."

After completing his diploma studies in biology and philosophy in 1988 (academic title Mag. rer. nat.), Huber turned to a completely different topic for his doctoral thesis, namely, pigeons' (*Columba livia*) ability to categorize complex visual classes. In comparison to students, pigeons solved a polymorphous classification problem (the so-called m-out-of-n problem) by learning to combine the four class-defining feature dimensions of an artificial stimulus set (so-called Brunswick faces) in an additive manner. Humans have difficulties solving such problems as quickly as pigeons because we tend to try combinations of conjunctive and disjunctive rules. Here again evolutionary epistemology offers an answer in terms of the parallel existence of simpler and more advanced, or in evolutionary terms older and more recent, processes of human cognition. Huber's work on categorization (prototype formation, feature learning) and concept formation (including abstraction and rule learning) remained the focus of his research for more than a decade after graduating (Dr. rer. Nat.) in 1991.

Ludwig Huber had the good fortune to be offered the position of university assistant to Prof. Riedl at the Institute of Zoology (Faculty of Natural Sciences) in 1991 and, after his retirement, became head of the Department of

Theoretical Biology for almost 8 years (1995–2003). Huber received the postdoctoral lecture qualification (habilitation) for zoology together with the professional upgrade to associate professor in 2000. Thanks to a successful period of raising third-party funding, and by means of international advertisements, Huber was able to hire qualified young postdocs and PhD students. These enthusiastic colleagues arrived with broad interests and helped to widen his research agenda and raising awareness of the steadily growing unit, its scientific output, and its international visibility, especially through an EU-funded international research project that he coordinated. As a result, his lab received the status of priority research program "Cognition" of the Faculty of Life Sciences in 2005.

Huber's purely noninvasive research program at the University of Vienna (1991–2011) involved many aspects of comparative cognition, clustering mainly around perceptual, social, and technical cognition. Rather than using animals as "model systems" to understand humans, he aimed at understanding the cognitive worlds of animals within an evolutionary context (Heyes and Huber 2000). Perhaps the most fundamental component of cognition is *categorization*. Using improved methodologies, Huber and his co-workers demonstrated that pigeons, though lacking language and presumably also the associated higher cognitive capacities, can categorize photographs or drawings as complex as those encountered in ordinary human experience (Huber et al. 2005). The underlying cognitive mechanisms include picture memorization, feature learning, prototype formation, and the abstraction of concepts. These topics had already been addressed in Huber's doctoral thesis, but he later added studies on the perception of biological motion (with Niko Troje, Kingston, Canada) to serve social recognition, picture-object equivalence, inference by exclusion, and the functional asymmetry of the pigeon brain (with Onur Güntürkün, Bochum, Germany). In addition to pigeons, the researchers investigated the link between perception and cognition in kea (*Nestor notabilis*), domestic dogs (*Canis familiaris*), red-footed tortoises (*Geochelone carbonaria*), lizards

(bearded dragon; *Pogona vitticeps*), archer fish (*Toxotes chatareus*), and giant pandas (*Ailuropoda melanoleuca*).

A second research focus clustered around social learning. This ability is considered an important manifestation of cognitive behavior in both humans and nonhuman species. Huber's main interest focused on the mechanisms underlying learning through conspecific observation and their contribution to the horizontal and vertical transmission of innovations. Rigorous experiments were conducted with marmosets (*Callithrix jacchus*) to investigate *imitation*, i.e., learning some part of the form of a demonstrated behavior (Voelkl and Huber 2000). Imitation, it is said, not only demands the most sophisticated cognitive processes but also enables the most elaborate form of social information transfer, "cultural transmission." The formation of behavioral traditions and possible effects of conformity and habit formation were studied in wild marmosets (with Nicola Schiel and Antonio Souto, Recife, Brasil). Other forms of nongenetic transmission, like *emulation* (i.e., learning about the properties or the function of objects), were studied in kea (with Michael Taborsky, Bern, Switzerland) (Huber et al. 2001). The functional role of observational learning and the learning of sequences was investigated in marmosets as well as dogs (Huber et al. 2009). In addition to evidence for automatic imitation (with Cecilia Heyes, London, UK) and *deferred* imitation (with Adam Miklosi, Budapest, Hungary), Huber and his team found evidence for *selective imitation* in dogs (with Gyorgy Gergely, Budapest, Hungary) (Range et al. 2007). Cooperation and some underlying social factors (like scrounging tolerance, inequity aversion) were studied in dogs, kea, and marmosets (Range et al. 2009). Concerning the evolution of social learning, they also found surprising evidence for social learning in nonsocial tortoises and lizards (Wilkinson et al. 2010).

The third research focus was directed at physical intelligence. In the inanimate environment, problems arise from the interaction with objects, the understanding of physics (*folk physics*), time, space, and causality. Using the kea as a model, the team investigated how birds manipulate objects in a flexible manner by learning how the objects affect the environment (Huber and Gajdon

2006). Comparisons with marmosets, but also ravens (*Corvus corax*) (with Thomas Bugnyar, Vienna), New Caledonian crows (*Corvus moneduloides*) (with Auguste von Bayern, Oxford, UK), and Goffin's cockatoos (*Cacatua goffiniana*) (with Alice Auersperg, Goldegg, Austria) provided important insights into the selective pressures for the evolution of technical intelligence. Both kea and Goffin's cockatoos showed flexible and innovative behavior, with the individual invention of using a stick tool to act in a goal-directed manner on objects. In collaboration with Elisabetta Visalberghi (Rome), Huber and his colleagues investigated causal understanding in capuchin monkeys (*Cebus apella*) using stones as percussors for nut-cracking behavior.

This extensive research agenda could not have been realized without the establishment of excellent facilities in cooperation with highly motivated collaborators. Firstly, Ulrike Aust and Michael Steurer helped establish a huge pigeon testing facility equipped with half- and fully automatized indoor conditioning units connected to outdoor aviaries for 120 pigeons. Ludwig Huber, along with Thomas Bugnyar and Bernhard Voelkl, established a marmoset lab with indoor/outdoor enclosures for two to three families of up to eight individuals each. Huber and Gyula Gajdon improved the outdoor facilities for kea (the mountain parrots of New Zealand) at the Konrad Lorenz Institute for Ethology. In 2007 Huber founded, with colleagues Friederike Range and Zsófia Virányi and the generous help of a private sponsor, the first Clever Dog Lab in Vienna. And finally, Anna Wilkinson's vision and enthusiasm made possible the creation of the "Cold Blooded Cognition" Lab in 2008, including indoor facilities for tortoises, lizards, and tadpoles.

In parallel to his research, Huber's teaching interests were also broadened, with lectures and courses ranging from animal behavior and cognition to comparative morphology, evolutionary biology, and even bioethics. He gave comparative cognition lectures not only at the University of Vienna but also as a guest professor at the Charles University in Prague (2005–2011) and at the University of Salvador de Bahia, Brazil (2012). Of

course, supervision comprised the majority of his teaching work, helping students on their way to becoming young scientists in more than 80 diploma or master projects and 30 doctoral or PhD projects.

In 2009, he helped recruiting two professors of cognitive biology (Tecumseh Fitch and Thomas Bugnyar) and with them established a new organizational unit, the Department of Cognitive Biology at the Faculty of Life Sciences. As its head from January 2010 to September 2011, Huber was responsible for founding a new research facility 40 km south of Vienna (the Haidlhof Research Station for Cognition and Communication Research) in cooperation with the University for Veterinary Medicine Vienna. In huge aviaries, altogether comprising 1300 m<sup>2</sup>, Thomas Bugnyar's and Huber's groups began comparative investigation of the social and technical abilities of corvids and kea (with Gyula Gajdon and Raoul Schwing). Furthermore, Tecumseh Fitch established research on the vocal production and perception of birds and mammals in specially equipped bioacoustics facilities.

In September 2011, Ludwig Huber was appointed professor of the Natural Science Foundations of Animal Ethics and Human-Animal Interactions at the new Messerli Research Institute, an interdisciplinary institution of the University of Veterinary Medicine Vienna, the Medical University of Vienna, and the University of Vienna. He was the head of comparative cognition and acted as the institute's spokesperson from its founding until 2014. This appointment allowed him to extend his previous work to the study of emotional processes like empathy, as well as to applied research, in particular on human-animal interactions and ethical issues (e.g., Müller et al. 2015). The range of study species extended to include some exotic species, which Huber and his team investigated in the lab and the field (Goffin's cockatoos with Alice Auersperg in Indonesia and poison frogs with Eva Ringler in French Guiana) and finally also farm animals (pigs, horses, chicken), which they started to investigate in semi-natural conditions (with Marianne Wondrak). Finally, Huber's theoretical interests opened the question of how our

understanding of cognitive and emotional processes in animals contributes to our concern and responsibility for them. He became convinced that the better people understand how animals think, decide, suffer, cooperate, reconcile, have empathy and theory of mind, etc., the more they will be inclined to respect and take care of them, i.e., take responsibility in the various forms of human-animal interactions and include them in our moral universe.

## Cross-References

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- ▶ [Behavioral Flexibility](#)
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## References

- Heyes, C. M., & Huber, L. (Eds.). (2000). *The evolution of cognition*. Cambridge, MA: MIT Press.
- Huber, L., & Gajdon, G. K. (2006). Technical intelligence in animals: The kea model. *Animal Cognition*, 9(4), 295–305. doi:10.1007/s10071-006-0033-8.
- Huber, L., Rechberger, S., & Taborsky, M. (2001). Social learning affects object exploration and manipulation in keas, *Nestor notabilis*. *Animal Behaviour*, 62(5), 945–954.
- Huber, L., Apfalter, W., Steurer, M., & Prossinger, H. (2005). A new learning paradigm elicits fast visual discrimination in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes*, 31(2), 237–246.
- Huber, L., Range, F., Voelkl, B., Szucsich, A., Viranyi, Z., & Miklosi, A. (2009). The evolution of imitation: What do the capacities of nonhuman animals tell us about the mechanisms of imitation? *The Philosophical Transactions of the Royal Society B*, 364, 2299–2309. doi:10.1098/rstb.2009.0060.
- Müller, C. A., Schmitt, K., Barber, A. L. A., & Huber, L. (2015). Dogs can discriminate emotional expressions of human faces. *Current Biology*, 25, 1–5. doi:10.1016/j.cub.2014.12.055.
- Range, F., Viranyi, Z., & Huber, L. (2007). Selective imitation in domestic dogs. *Current Biology*, 17, 1–5. doi:10.1016/j.cub.2007.04.026.
- Range, F., Horn, L., Viranyi, Z., & Huber, L. (2009). The absence of reward induces inequity aversion in dogs. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 340–345. doi:10.1073/pnas.0810957105.
- Voelkl, B., & Huber, L. (2000). True imitation in marmosets. *Animal Behaviour*, 60(2), 195–202. doi:10.1006/anbe.2000.1457.
- Wilkinson, A., Kuenstner, K., Mueller, J., & Huber, L. (2010). Social learning in a non-social reptile (*Geochelone carbonaria*). *Biology Letters*, 6(5), 614–616. doi:10.1098/rsbl.2010.0092.



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## Pinniped Life History

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The term pinniped comes from the Latin *pinna* for “fin” or “feather,” and *pedis* for “footed.” The taxonomic grouping Pinnipedia is not its own order, but rather is classified within the order Carnivora and consists of three families of marine mammals: Phocidae which are the true seals (i.e., earless seals), Otariidae, the sea lions and fur seals (i.e., eared seals), and Odobenidae, the walrus. Otariids are most easily distinguished by their external ear or pinnae, their large fore-flippers, and the ability to rotate their pelvis on land and walk quadrupedally. Phocids are distinguished by a lack of pinnae, their short, fur covered fore-flippers which have pronounced claws, and their inability to rotate their pelvis to walk quadrupedally on land. Odobenids are easily recognized by their general lack of fur and their pronounced tusks present on both the male and female walrus. Like the Otariids, they can walk quadrupedally on land (see Fig. 1). Taken together there are 33 extant species of pinnipeds which can be found in almost all marine waters of the globe, though distribution patterns can be seen between groups. Only phocids are found in the Arctic and

Antarctic with the exception of the walrus (found in northern circumpolar waters). Most fur seal populations are restricted to the southern hemisphere, yet most other otariids are found in both hemispheres. The Hawaiian (*Monachus schauinslandi*) and Mediterranean monk seals (*Monachus monachus*) are the only tropic species, and the Baikal seal (*Pusa sibirica*) is the only freshwater species. While pinnipeds inhabit all climate zones, they are not currently in the waters off the coast of Asia or India, and it is suggested that these waters are nutrient poor and therefore do not have a stable food supply for them (Riedman 1990).

## Evolution

Pinnipeds are thought to have evolved from their terrestrial ancestors, a group termed the Canoidea. Since Canoidea consists of multiple groups such as the ursids (bears), mustelids (weasels and otters), and canids (dogs), there has historically been argument within the scientific community as to the specific phylogenetic origins of the three pinniped families (Arnason et al. 2006; Lowenstein 1986; for a recent in-depth review of the debate see Koretsky et al. 2016). There are two views of their ancestry centered around the question of whether pinnipeds evolved from the same, or two different, phylogenetic lines. The diphyletic view states that both otariids and odobenids evolved from a bear-like ancestor around 25



**Pinniped Life History, Fig. 1** Photographs of three-species representative of the three pinniped families: (a) Family Phocidae, *Phoca vitulina* (harbor seal); (b) Family Otariidae, *Zalophus californianus* (California sea lion); (c) Family Odobenidae, *Odobenus rosmarus* (walrus)

(Photo credits: Candyce Paparo, Long Island Aquarium & Exhibition Center/Center for the Study of Pinniped Ecology & Cognition (a, b); Center for the Study of Pinniped Ecology & Cognition (c))

million years ago (MYA) in the early Miocene while the phocids evolved from a mustelid or otter-like ancestor about 20 MYA, mid-Miocene (Koretsky and Holec 2002; Koretsky and Sanders 2002; Koretsky and Barnes 2003; Repenning 1976; Riedman 1990). While this view has been supported by the fossil record, recent molecular evidence (e.g., DNA and RNA from extant species) suggests a monophyletic view with phocids and otariids descending from a common bear-like ancestor approximately 25 MYA (early Miocene) (Arnason et al. 2006; Dasmahapatra et al. 2009; Higdon et al. 2007, 2008) Despite conflicting evidence between the fossil record and molecular data, the current scientific consensus is the monophyletic view emphasizing a common ancestor; however, there is still some debate as to whether their most recent common terrestrial ancestors are ursids (bears) or mustelids (weasels/otters) (Berta and Churchill 2012; Boness and Bowen 1996).

Currently, of the 33-extant species of pinnipeds, four phocids and one otariid are listed as endangered with five phocid and two otariids listed as threatened (United States Fish and Wildlife (USFW) 2017). The Caribbean (or West Indian) monk seal (*neomonachus tropicalis*) was listed as threatened on March 11, 1967, and officially declared extinct as of October 28, 2008, being removed from the Federal Register after there had been no reported sightings of the seal in 50 years (USFW 2016). The Hawaiian monk seal (*Monachus schauinslandi*) was listed as endangered as of June 2, 1970 (USFW 2017),

and critically endangered in 2008 (Karamanlidis and Dendrinis 2015; Littnan et al. 2015) with the recent population estimates at 1,112 individuals (National Oceanic and Atmospheric Administration (NOAA) 2015). While many pinniped populations are thriving, the factors influencing the 12 species listed as threatened or endangered is the focus of many research and conservation efforts. Data show that the species' populations most in danger are those that inhabit the subtropical/tropical and Arctic/Antarctic regions of the globe (i.e., the more northern and southern latitudes), with more temperate dwelling species having stable and even thriving populations (Ferguson and Higdon 2006). This suggests that the more extreme areas of the globe may be more susceptible to both natural and man-made changes in the ecosystem. The underlying causes of this relationship between latitude and population stability is an area of research with investigations focused on the interactions between ecology and the life history of these varied pinniped species with an emphasis on climate change and prey distribution/availability (Ferguson and Higdon 2006).

The life history of pinnipeds is especially multidimensional because they are amphibious marine mammals that carry out critical life functions both on land and in the water. Their evolutionary ties to their terrestrial ancestors are demonstrated by their dependence on the sea for foraging while often breeding and giving birth on land. While the challenges of individual species

vary, there are several generalizations that can be made within the life history of pinnipeds as a group with major differences being drawn between the phylogenetic lines of the phocids and otarioids (both the otariids and odobenids).

## Life Span

The life span of pinniped species ranges from 15 to 30 years with males having a shorter span due to the added biological stressors and potential injuries incurred during male-male aggressive encounters (see Table 1). It has been shown that many northern elephant seals (*Mirounga angustirostris*) die before reaching sexually maturity (age five) and significantly more die before reaching age nine at which time they are considered able to successfully compete for females and reproduce (Le Boeuf 1981; Reiter et al. 1981).

As mentioned above, it should be noted that chronological age of reproductive maturity (age at which they are physically capable of breeding) is different than the age at which an animal successfully breeds. Typically, females breed once they hit sexually maturity (e.g., age two), but they may not give birth for a few more years (e.g., 4–5 years of age) (Boness et al. 2002; Riedman 1990). This discrepancy in age is more pronounced in male pinnipeds, perhaps because they must be physically capable of breeding, as well as physically large enough and behaviorally mature enough, to compete for territory/females. For example, walrus (*Odobenus rosmarus*) reach sexual maturity at 9–10 years of age but may not breed successfully until 13–16 years old (Fay 1982).

## Reproduction

Overall, both male and female pinnipeds must have sufficient mass and a healthy body condition, as well as the behavioral maturity, to breed successfully and reproduce. Sexually mature pinnipeds typically come ashore to their natal beaches (the site at which they were born) each year to give birth and then mate (Hoffman and Forcada 2012). Most otariids breed and give birth on land (Boness

1991; Franco-Trecu et al. 2015; Giardino et al. 2016), while 15 of the 18 phocid species mate aquatically (for an extensive review of aquatic breeding phocids see Van Parijs 2003). Most exceptions seem to be the ice seals, though data exist for a limited number of species. For example, evidence suggests that weddell seals (*Leptonychotes weddellii*) do not return to breed at the site where they were born (Davis et al. 2008), and they are the only large phocid to breed exclusively on fast-ice (i.e., ice attached to land). This may be due to female movement being restricted to consistent breathing holes in the ice (Cline et al. 1971; Bartsch et al. 1992; Harcourt et al. 1998, 2000).

As amphibious marine mammals, access to land for mating and/or birthing is critical and therefore timing of the annual breeding/pupping season is important. Female estrous cycles (when females are physiologically receptive for breeding) are annually synchronous for all pinnipeds, and mating occurs relatively quickly after the birthing or parturition process. Though this timeframe between birthing and mating ranges somewhat among species, pinnipeds manage to synchronize in part through embryonic diapause or delayed implantation (Pomeroy 2011). In this way, the egg is fertilized and develops for approximately 7–10 days at which point development pauses at the blastocyst stage. Up to several months later (timing depending on the species), the embryo begins to develop again and implants into the uterus. This delay allows for the gestation period (including the diapause) to last approximately 10–12 months, ensuring that sexually mature males and receptive females arrive at their breeding sites at the same time each year.

Females give birth to one offspring per year of sexual maturity, though this is in part dependent on environmental factors such as food supply. Females may not give birth in a certain year if there are not enough resources available and her body is not in a healthy condition to sustain a pregnancy and lactation period (Boyd 2000; Shero et al. 2015). Twinning is rare, though has been documented (Hoffman and Forcada 2009; Riedman 1990), but research suggests that having twins may be detrimental as it decreases overall

**Pinniped Life History, Table 1** Information on 26 of the 33 extant species of pinnipeds. The data provide descriptions of general aspects of life history, organized by taxonomic family, including average mass of males and females of a species, existence of sexual dimorphism, life span, breeding strategy, lactation length, and percent milkfat. These data allow one to compare not only across species but across and within the phocid, otariid, and odobenid families. There is not sufficient data reported to provide a valid average of milkfat when “nd” is indicated in the table

Common name <i>Scientific name</i>	Ave female mass	Ave male mass	Sexual dimorphism	Life span (yrs)	Breeding strategy	Ave lactation length	Ave % milkfat	Source <sup>a</sup>
<b>Phocidae</b>								
Baikal seal	130 kg	130 kg	No	50–55	Monogamy	2 months	nd	1, 2, 3
<i>Pusa sibirica</i>								
Bearded seal	260–360 kg	260–360 kg	Slight; females larger	25	Monogamy/Slight polygyny	2–3 weeks	49	4, 5, 6
<i>Erignathus barbatus</i>								
Grey seal	250 kg	400 kg	Yes	25–35	Moderate polygyny/ Ice breeders monogamous	2–3 weeks	60	7, 8, 9, 6
<i>Halichoerus grypus</i>								
Harbor seal	110 kg	110 kg	No	25–30	Slight polygyny	3–4 weeks	50	6, 9
<i>Phoca vitulina</i>								
Harp seal	135 kg	135 kg	No	Unknown	Slight polygyny	12 days	57	6, 10, 11, 12
<i>Pagophilus groenlandicus</i>								
Hawaiian monk seal	170–205 kg	170–205 kg	Slight; females larger	25–30	Slight polygyny	4–6 weeks	nd	3, 6, 13
<i>Monachus schauinslandi</i>								
Hooded seal	200 kg	300 kg	Yes	30–35	Slight polygyny	3–5 days	61	6, 14, 15

<i>Cystophora cristata</i>																						
Mediterranean monk seal	240–400 kg	240–400 kg			Slight; males larger	20–25	Slight polygyny	4 months	nd	nd												3, 6, 16, 17
<i>Monachus monachus</i>																						
Northern elephant seal	600 kg	2000 kg			Yes	13–19	Extreme polygyny	3–4 weeks	54	54												6, 18, 19
<i>Mirounga angustirostris</i>																						
<b>Phocidae</b>																						
Ribbon seal	80 kg	80 kg			No	20–30	Slight polygyny	3–5 weeks	nd	nd												3, 6, 20
<i>Histiophoca fasciata</i>																						
Ringed seal	50–70 kg; 110 kg for Saimaa subspecies	50–70 kg; 110 kg for Saimaa subspecies			No	25–30	Monogamy/Slight polygyny	6 weeks	42	42												6, 21, 22, 23
<i>Phoca hispida</i>																						
Southern elephant seal	400–900 kg	1–2 tonnes			Yes	10–20	Extreme polygamy	3 weeks	40	40												3, 24, 25
<i>Mirounga leonina</i>																						
Spotted seal	65–115 kg	65–115 kg			No	30–35	Monogamy/Slight polygyny	5–6 weeks	nd	nd												6, 26
<i>Phoca largha</i>																						
Weddell seal	1200 lbs. (544 kg)	544 kg			No	20–30	Slight/Moderate polygyny	7 weeks	48	48												6, 27
<i>Leptonychotes weddellii</i>																						
<b>Otariidae</b>																						
Antarctic fur seal	22–50 kg	130–200 kg			Yes	15–25	Moderate polygyny	4 months	42	42												3, 28, 29, 30

(continued)

Pinniped Life History, Table 1 (continued)

Common name <i>Scientific name</i>	Ave female mass	Ave male mass	Sexual dimorphism	Life span (yrs)	Breeding strategy	Ave lactation length	Ave % milkfat	Source <sup>a</sup>
<i>Arctocephalus gazella</i>								
Australian sea lion	61–105 kg	180–250 kg	Yes	20–25	Moderate polygyny	11–12 months	nd	3, 31, 32, 33
<i>Neophoca cinerea</i>								
California Sea Lion	110 kg	315 kg	Yes	20–30	Moderate polygyny	10 months	44	3, 6, 34
<i>Zalophus californianus</i>								
Galapagos fur seal	27–28 kg	60–68 kg	Yes	20–25	Moderate polygyny	18 months	29	35, 36
<i>Arctocephalus galapagoensis</i>								
<b>Otariidae</b>								
Guadalupe fur seal	40–50 kg	160–180 kg	Yes	20	Moderate polygyny	9 months	nd	6, 37
<i>Arctocephalus townsendi</i>								
New Zealand sea lion	90–165 kg	300–450 kg	Yes	~20	Extreme polygyny	12 months	nd	3, 38, 32
<i>Phocarcos hookeri</i>								
Northern fur seal	60 kg	270 kg	Yes	10–27	Extreme polygyny	4–5 months	42	6, 39, 40



<i>Callorhinus ursinus</i>														
Southern sea lion	170 kg	300–350 kg	Yes		15–20	Moderate polygyny	11–12 months	47				3, 41, 42, 43		
<i>Otaria byronia</i>														
Steller sea lion	350 kg	1120 kg	Yes		20–30	Extreme polygyny	11–12 months	24				3, 6, 44		
<i>Eumetopias jubatus</i>														
Subantarctic fur seal	25–67 kg	70–165 kg	Yes		15–20	Moderate polygyny	11 months	42				3, 45, 46		
<i>Arctocephalus tropicalis</i>														
<b>Odobenidae</b>														
Walrus	580–1039 kg	880–1557 kg	Yes		30–40	Polygyny	2–3 years	30				5, 6, 47, 48		
<i>Odobenus rosmarus</i>														

<sup>a</sup>1, Nomokonova et al. 2013; 2, Pastukhov 1990; 3, Riedman 1990; 4, Burns 1981a; 5, Fay 1982; 6, NOAA 2016; 7, Amoroso et al. 1950; 8, Boness and James 1979; 9, Fedak and Anderson 1982; 10, Bowen and Sergeant 1983; 11, Kovacs and Lavigne 1986; 12, Oftedal et al. 1993; 13, Alcorn and Buelna 1989; 14, Bowen et al. 1985; 15, Kovacs and Lavigne 1992; 16, Aguilar et al. 2007; 17, Pomeroy 2011; 18, Crocker et al. 2001; 19, Reiter et al. 1978; 20, Burns 1981b; 21, McLaren 1958; 22, Hammill et al. 1991; 23, Zhang et al. 2014; 24, Carrick et al. 1962; 25, Hofmeyr 2015a; 26, Boveng 2016; 27, Kaufman et al. 1975; 28, Payne 1979; 29, Kerley 1985; 30, Doitge et al. 1986; 31, Goldsworthy 2015; 32, Marlow 1975; 33, Ling and Walker 1976; 34, Stewarts and Yochem 1984; 35, Trillmich 1979; 36, Trillmich and Lechner 1986; 37, Gallo-Reynoso and Figueroa-Carranza 1996; 38, Chivers 2015; 39, Peterson 1965; 40, Costa and Gentry 1986; 41, Cárdenas-Alayza et al. 2016; 42, Hamilton 1934; 43, Vaz-Ferreira and Ponce de Leon 1987; 44, Costa 1991; 45, Hofmeyr 2015b; 46, Roux and Hess 1984; 47, Kastelein et al. 2014; 48, Lowry 2016

survival rates (Schultz et al. 2011). Alloparenting, a system in which individuals in the population other than the mother contribute to the care of the offspring, is rare but has been observed in the pinnipeds (Boness and Bowen 1996; Porter and Trites 2004; Schulz and Bowen 2005). It is most likely to occur when a female has lost her pup and fosters one that has lost its mother. Rarely, females will nurse a stray pup alongside its own. Males do not offer paternal care and, as stated, females do not usually care for offspring that are not their own. In fact, females have been known to behave aggressively toward nonfilial pups attempting to nurse. Infanticide has been observed but is usually caused by a nonfilial pup continuing to approach and attempt to nurse from an aggressive female, or by incidental injury due to proximity of an aggressive male-male interaction, though males have been known to kill pups through directed aggressive contact (Kiyota and Okamura 2005).

### Breeding Strategies

The details of mating strategies vary between species but most are polygynous and fall under either of two categories: harem or lek breeding systems (for a more detailed review see also Boness et al. 2002). In a harem system, the males fight for dominance rankings and access to receptive females on the beach. The most dominant male will spend the breeding season alternating between mating with many females and fighting off male challengers. Due to the physical nature of the male-male competition, many do not mate successfully until they are approximately 10 years old, even though sexual maturity may have been reached at 4 years of age (see “Life Span”). Males must acquire the size and the experience to win fights with the older, more dominant, males each year to gain access to females. For example, male northern elephant seals herd females inside their territory and keep other males out while male California sea lions (*Zalophus californianus*) compete to control specific locations on the beach. Unlike elephant seals, the female sea lions are free to move between these areas and therefore from male to male. Conversely, male harbor seals (*Phoca vitulina*) demonstrate a lek system and do not tend to have

physical altercations with each other during the breeding season, but rather vocalize underwater to claim a territory therefore advertising their presence to females and deterring other males from that area (Van Parijs 2003). This difference in breeding style may be related to resource availability (food and breathing holes for ice seals), mating location (females of species that mate aquatically have more control over their mate choice), and the extent of sexual dimorphism (difference in physical size between males and females) found between various species (Van Paris 2003; González-Suárez and Cassini 2014; Modig 1996). Elephant seals have the largest degree of sexual dimorphism with the female northern elephant seals being an average of 1,300 pounds (600 kg) and males three to five times that at an average of 4,400 pounds (2,000 kg) (see Table 1). Their breeding strategy consisting of males fighting, often violently, to attain dominance and control of females favors the evolution of a large body size. Harbor seals, on the other hand, demonstrate little to no sexual dimorphism, with males and females both averaging 245 pounds (110 kg), and they demonstrate little to no male-male aggression during the breeding season.

Reproductive success rates are based on number of offspring produced throughout the life span. While this is well defined and relatively easy to quantify for females of a given species, the data is less discernable for males. Regardless of the breeding strategy employed by a species, females give birth to one offspring per year (as noted, twins are rare and most do not survive to maturity), but males mate with multiple females each season making DNA testing the most reliable way to determine paternity and male success rate in a population. Due to the inherent difficulty of DNA testing for male success rates each year, most estimates are based on observed successful copulations and known dominance ranking of individual males. While this seems a reasonable assessment of male success, some data indicate that the most dominant males may not necessarily be providing the DNA for all offspring. For example, in northern elephant seals, “sneaker” males (young juveniles that “sneak” a copulation with a

female) have been found to have contributed DNA to the population despite their lower dominance ranking and smaller size (de Bruyn et al. 2011). They have been successful in mating with females on the outer edges of a harem while the dominant male is engaged in a copulation, a fight with another male, or sleeping (hence the term sneaker male). This is interesting to note in relation to the evolution of behavioral/cognitive strategies in pinniped species.

### Maternal Dependency/Lactation

Care of offspring in pinnipeds centers around females and consists of protection from predators but primarily lactation or milk production. The mother-pup bond is strong during the lactation period and decreases significantly, and perhaps completely, after weaning. However, there is evidence that females behave in an affiliative manner with their kin when returning to their natal beaches to breed each year (Insley et al. 2003; Schusterman et al. 2002), and there is some evidence that a California sea lion and its mother recognized each other for many years (Hanggi and Schusterman 1990).

Length of maternal dependence and lactation is generally divided between pinniped families, though it should be noted that other factors such as body size, ecology, foraging strategy, breeding/birthing location, and substrate all play an integrated role in the lactation strategy displayed by a given species (Bartholomew 1970). The phocids have the shortest lactation period ranging from four days (hooded seal, *Cystophora cristata*) to two and one half months (Baikal seal, *Pusa sibirica*; Pastukhov 1993), with a milk containing 40–50% fat (see Table 1). Otariids have a moderate nursing period between 4 months and 3 years with approximately 20–35% milkfat, while odobenids average a 2–3 year lactation period with about 30% milkfat, making them the pinniped with the longest period of maternal care (see Table 1). In fact, the walrus is the only species to have adopted a strategy of nursing their young in the water and having their young accompany them on foraging trips (Schulz and Bowen 2005). Therefore, three predominant lactation strategies (discussed below) can be seen among

female pinnipeds which are generally divided among phylogenetic lines (and will be discussed as such for purposes of generalizing here), though the interactions between species ancestry, maternal mass, breeding substrate, thermoregulation challenges, milk composition, and various other ecological factors must not be overlooked (for a detailed review see Schulz and Bowen 2005).

A *fasting strategy* with little to no feeding is employed by phocids, though the harbor seal and ringed seal (*Phoca hispida*) have been documented to occasionally forage during this time. This may be correlated with their smaller body size, creating an inability to maintain enough energy reserves of their own throughout lactation (Boness and Bowen 1996; Bowden et al. 1992). This foraging during lactation may also be related to the availability of food close to shore, which may entice them to feed later in the lactation period (Boyd 1998). Length of lactation period is correlated with maternal mass and percent of milk fat. The shorter the lactation period (for all pinnipeds), the more quickly fat reserves must be transferred to pups in the form of milk. Therefore, larger females can handle dumping more fat rich milk into their pups quickly. Of course, longer lactation periods mean more maternal care/time for pup growth and protection from predators; however, if fasting, there will always be an upper limit by which the female must return to sea or risk decreasing her reserves to the point by which she can no longer survive.

Ice-breeding phocids fast and have the shortest lactation periods of all pinnipeds, an advantage in an environment where a mother and pup are together on either fast (attached) or pack (floating) ice. For example, if the ice were to crack, break, and/or float away, a foraging female may not be able to find her pup upon returning to the ice. Breaking ice could crush or drown a pup. Also, in an extremely cold climate, adding blubber to a pup as quickly as possible will help it to thermoregulate appropriately.

Otariids have adopted a *foraging-cycle strategy* meaning that they alternate, or cycle, between nursing and foraging throughout the lactation period. This allows for a longer duration of maternal care, as the females replenish their energy

reserves between nursing bouts. Whether this strategy is advantageous because it allows them to care for their pups for longer periods of time while not overly depleting their own reserves, or if it is more energetically demanding in the long run, is an area of continued study (Coltman et al. 1997; see Schulz and Bowen 2005). Perhaps the otariids, being small bodied as compared to most phocids, simply cannot acquire the energy reserves needed for fasting while lactating. These foraging bouts also add another challenge for these mother-pup pairs, as the pups are left alone in the rookery while the mother goes to sea to forage for 2–3 days. When the female returns after a foraging trip of 1–6 days, she and her pup must overcome the challenge of reuniting among hundreds of other mother-pup pairs (see Insley 2000; Trimble and Insley 2010).

A third strategy, the *aquatic nursing strategy*, is only found in the odobenids. The walrus, having the longest period of maternal care (2–3 years), has adopted a strategy of nursing in the water, as opposed to exclusively on land, and pups are known to accompany their mothers on foraging trips (Boness and Bowen 1996; Fay 1982). Walrus pups are born the least precocious of the pinnipeds, and this lengthy dependence on the mother allows for a longer maturation process of the pup prior to survival on its own.

## Foraging

The majority of a pinniped's fresh water supply is extracted from the food they eat and some is acquired through the metabolism of their blubber layer. Pinnipeds have been known to consume salt water in small amounts and metabolize it ending with a freshwater gain, but the process requires a lot of energy and is not an efficient source of hydration (Riedman 1990).

Pinnipeds tend to be generalists with diets consisting primarily of fish, crustaceans, and cephalopods and are typically solitary hunters though they have been documented hunting cooperatively when herding a large school of fish (Gales et al. 2004; Riedman 1990). A few species are specialists and as such have adaptations for

feeding on certain prey items. For example, the crabeater seal (*Lobodon carcinophagus*) eats krill, and its teeth are formed in a way that allows them to gulp water and strain it out leaving the krill in their mouths on which to feed. Bearded seals (*Erignathus barbatus*) and walrus feed on mollusks and other bottom dwelling invertebrates. They both have substantial vibrissae, or whiskers, with which they use for rooting through muddy substrates and the walrus' mouth can produce suction strong enough to pull mollusks out of their shells. Ringed seals feed primarily on crustaceans and elephant seals prefer squid. The leopard seal (*Hydrurga leptonyx*), found in Antarctica, eats penguins and is the only pinniped known to prey on other seals (typically young crabeater seals) (Hocking et al. 2013).

Foraging occurs at varying depths and durations based on species, but a notable mention with significant diving abilities is the elephant seal, known to make foraging dives to an average depth of 1,680 feet (512 m) and 22 min in length (Heerah et al. 2014). The elephant seals' maximum recorded dive depth is 6,562 feet (2,000 m) and for a duration of approximately two hours, rivalling that of the sperm whale, making it one of the deepest diving marine mammals. These long dives are in part possible due to their large size which increases the amount of oxygen they can store and therefore increasing time spent at depth and decreasing the need to come up for air frequently.

As amphibious mammals, pinnipeds must balance the energetic resources needed to leave a terrestrial haul-out location and actively search and hunt for food with the energy gained by the food they consume. Foraging patterns are correlated with, and generally divided by, ancestry with the phocids most likely to employ an *income strategy* and otarioids using a *capital strategy* (Arthur et al. 2016; Stephens et al. 2014). For example, the hooded seal (a phocid) tends to favor a capital strategy based on fewer trips with longer travel distances to and from foraging sites of large density prey (through which they increase reserves in body mass – creating capital reserves), while the California sea lion (an otariid) favors an income strategy with shorter, but more frequent,

foraging trips (less reserve and more frequent income replenishment needed). The quality of prey is also important as traveling a long distance for many poor-quality fish will not be energetically advantageous over traveling a shorter distance for fewer fish, if the smaller fish population is a much higher quality. Latitude ranges will, in part, determine prey distribution with colder/temperate waters, and therefore middle latitudes, having higher productivity and prey item availability.

Therefore, factors correlated with a capital versus income foraging strategies (and with the phocid and otarioid groups, respectively) are the species' overall body size, maternal care/lactation strategy (see "[Reproduction](#)"), and global distribution. Whether the driving factors of strategy are ancestry, physical properties of the species (e.g., overall size and depth of blubber layer), water temperature and quality, or habitat ecology including prey availability/distribution is an active area of research. These factors are inherently interconnected and it is probable that rather than a direct causal link, the best predictor of foraging strategy will be an interactive model of the aforementioned variables.

## Molting

Molting is another event tethering these amphibious marine mammals to land. All species molt, during which time they undergo a relatively drastic shedding of their fur accompanied by the growth of a new coat. The timing of the molt depends on the species as well as the age within species. For example, molting is staggered by age in the northern elephant seal with yearlings hauling out in the fall, adult females in the spring after foraging trips following the breeding season, and adult males molting in the summer (Longstreth 2016; Riedman 1990). Pups of all species go through an initial molt of their lanugo, which is a layer of fur that develops in utero and serves to help newborn pups maintain their core body temperature until their blubber reserves have increased. Some pups (e.g., the harbor seal) shed their lanugo in utero (prior to birth), but most

pinnipeds shed it by the end of weaning (Bruemmer 1975; Riedman 1990).

While many terrestrial mammals are known to shed throughout the year with marked changes in this based on seasonality/temperature, the pinniped molt is notably different in large part due to their semiaquatic lifestyle. The growth of new fur requires increased blood flow to the surface of the skin. This is counter to the needs of marine mammals in that they often shunt blood away from the surface to their core (major organs and large muscles) to limit heat loss to the aquatic environment (Erdsack et al. 2012). Therefore, growing new fur and maintaining their core body temperature are essentially at odds. Many pinnipeds compensate for this by not shedding and growing hair continuously throughout the year, but rather by condensing this process into a yearly event or molt. During this time, they remain on land for relatively long periods of time allowing the blood to remain at the surface of the skin providing the nutrients needed for new hair growth.

Among the pinnipeds two main molting strategies emerge: one being to increase body mass (foraging), then fast and remain out of the water (more blood supply to the skin/new fur) allowing for a short molt duration, while the second is to continue to forage throughout the molt, entering the water (interrupted blood supply to the skin/new fur), thus requiring a longer molt duration. Which strategy is employed can be generalized as a division between the phocid and otarioid lines. Harbor seals (a phocid) have relatively short molts lasting on average 1 month while the molt of a California sea lion (an otariid) can last up to a few months with a peak in shedding lasting a month or more. However, it must be noted that there are many interacting variables underlying reliance on these strategies other than ancestry (see "[Foraging](#)").

An extreme strategy in the phocid line is employed by elephant seal species and the Hawaiian monk seal. They haul out once per year and not only shed their fur but their skin as well. Large patches of their hair and skin peel off to reveal new skin and fur below. This process has been term a *catastrophic molt* and requires a lot of energy and a large blood supply to the surface of

the body (Ling 1970). Therefore, these seals fall under the category of a short duration molt during which time they fast and remain on the beach until its completion.

## Migrations

Pinnipeds have a consistent and annual migratory pattern primarily based on feeding, breeding/birthing, molting, and seasonal ice (for the Arctic/Antarctic species) (see Luschi 2013). They migrate to breed and give birth, traveling to warmer waters for the new pups that lack a thick blubber layer for thermoregulation and then to cooler waters with greater productivity and more prey items. An exception to this are many of the ice seals as they prefer to breed when the ice is most prevalent allowing for larger areas for breeding and pupping and a lowered chance of fast ice breaking off and becoming a moving ice floe. If this were to happen during the weaning period, females could be separated from their pup (see “Reproduction”).

The methods by which pinnipeds navigate during these migrations are not completely understood. Researchers believe that it is a combination of their ability to use underwater landmarks, water and wind currents, water temperature, and even celestial bodies. Mauck et al. (2008) found that the harbor seal can utilize the stars in the night sky to navigate, and Ronald and Healey (1981) found that juvenile harp seals (*Pagophilus groenlandicus*) are successful on their annual northern migration (up to about 3,100 miles/5,000 km) on their first trip with no adult seal present. This indicates that, at least in some cases, aspects of these migrations may be innate.

## Conclusion

The life history of a species encompasses a pattern of resource acquisition and utilization in support of the interactions between lifespan, foraging, and reproduction strategies (which may or may not include migratory patterns in relation to prey

and/or mate availability and access). This interrelated web of factors is based on the evolutionary history of a species, the past and present environmental pressures, and the ecological systems in place. The above sections are an overview of the basic points of life history within the pinnipeds but, as with any taxonomic group, the physiological and behavioral aspects of these animals are not only influenced by the past and current environments but will continue to be shaped by their environments to come.

## Cross-References

- ▶ [Pinniped Cognition](#)
- ▶ [Pinniped Communication](#)
- ▶ [Pinniped Diet](#)
- ▶ [Pinniped Locomotion](#)
- ▶ [Pinniped Morphology](#)
- ▶ [Pinniped Navigation](#)
- ▶ [Pinniped Sensory Systems](#)

## References

- Aguilar, A., Cappozzo, L. H., Gazo, M., Pasto, T., Forcada, J., & Grau, E. (2007). Lactation and mother-pup behaviour in the Mediterranean monk seal *Monachus monachus*: An unusual pattern for a phocid. *Journal of the Marine Biological Association of the UK*, 87, 93–99. doi:10.1017/S0025315407056147.
- Alcorn, D. J., & Buelna, E. K. (1989). The Hawaiian monk seal on Laysan Island. NOAA Technical Memorandum, NMFS.
- Amoroso, E. C., Goffin, A., Halley, G., Mathews, L. H., & Mathews, D. J. (1950). Lactation in the grey seal. *Journal of Physiology*, 113, 4–5.
- Arnason, U., Gullberg, A., Janke, A., Kullberg, M., Lehman, N., Petrov, E. A., & Väinölä, R. (2006). Pinniped phylogeny and a new hypothesis for their origin and dispersal. *Molecular Phylogenetics and Evolution*, 41 (2), 345–354. doi:10.1016/j.ympev.2006.05.022.
- Arthur, B., Hindell, M., Bester, M. N., Oosthuizen, W. C., Wege, M., & Lea, M. (2016). South for the winter? Within-dive foraging effort reveals the trade-offs between divergent foraging strategies in a free-ranging predator. *Functional Ecology*, 30(10), 1623–1637. doi:10.1111/1365-2435.12636.
- Bartholomew, G. A. (1970). A model for the evolution of pinniped polygyny. *Evolution*, 24, 546–559. doi:10.2307/2406835.



- Bartsch, S. S., Johnston, S. D., & Siniff, D. B. (1992). Territorial behavior and breeding frequency of male Weddell seals (*Leptonychotes weddellii*) in relation to age, size, and concentration of serum testosterone and cortisol. *Canadian Journal of Zoology*, *70*, 680–692. doi:10.1139/z92-102.
- Berta, A., & Churchill, M. (2012). Pinniped taxonomy: Review of currently recognized species and subspecies, and evidence used for their description. *Mammal Review*, *42*(3), 207–234. doi:10.1111/j.1365-2907.2011.00193.x 4.
- Boness, D. J. (1991). Determinants of mating systems in the Otariidae (Pinnipedia). In: Renouf D (Ed) Behaviour of pinnipeds (pp.1–44). London: Chapman & Hall. doi:10.1007/978-94-011-3100-1\_1.
- Boness, D. J., & Bowen, W. D. (1996). The evolution of maternal care in pinnipeds. (cover story). *Bioscience*, *46*(9), 645–654. doi:10.2307/1312894.
- Boness, D. J., & James, H. (1979). Reproductive behaviour of the Grey seal (*Halichoerus grypus*) on Sable Island, Nova Scotia. *Journal of Zoology*, *188*(4), 477–500. doi:10.1111/j.1469-7998.1979.tb03430.x.
- Boness, D. J., Clapham, P. J., & Mesnik, S. L. (2002). Life history and breeding strategies. In A. R. Hoelzel (Ed.), *Marine mammal biology: An evolutionary approach* (pp. 278–324). Malden: Blackwell.
- Bowden, W. D., Oftedal, O. T., & Boness, D. J. (1992). Mass and energy transfer during lactation in a small phocid, the harbor seal (*Phoca vitulina*). *Physiological Zoology*, *65*, 844–866. doi:10.2307/30158543.
- Bowen, W. D., & Sergeant, D. E. (1983). Mark-recapture estimates of harp seal pup (*Phoca groenlandica*) production in the northwest Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences*, *40*, 728–742. doi:10.1139/f83-095.
- Bowen, W. D., Oftedal, O. T., & Boness, D. J. (1985). Birth to weaning in four days: Remarkable growth in the hooded seal. *Cystophora cristata*. *Canadian Journal of Zoology*, *63*, 2841–2846. doi:10.1139/z85-424.
- Boveng, P. 2016. *Phoca largha*. The IUCN Red List of Threatened Species 2016: e.T17023A45229806. Retrieved on February 21, 2016 from <http://dx.doi.org/10.2305/IUCN.UK.2016-1.RLTS.T17023A45229806.en>.
- Boyd, I. L. (1998). Time and energy constraints in pinniped lactation. *American Naturalist*, *152*(5), 717–728. doi:10.1086/286202.
- Boyd, I. L. (2000). State-dependent fertility in pinnipeds: Contrasting capital and income breeders. *Functional Ecology*, *14*(5), 623. doi:10.1046/j.1365-2435.2000.t01-1-00463.x.
- Bruemmer, F. (1975). A year in the life of a harp seal. *Natural History*, *84*(4), 42.
- de Bruyn, P. N., Tosh, C. A., Bester, M. N., Cameron, E. Z., McIntyre, T., & Wilkinson, I. S. (2011). Sex at sea: Alternative mating system in an extremely polygynous mammal. *Animal Behaviour*, *82*(3), 445–451. doi:10.1016/j.anbehav.2011.06.006.
- Burns, J. J. (1981a). Bearded seal – *Eringnathus barbatus*. In S. H. Ridgeway & R. J. Harrison (Eds.), *Handbook of marine mammals. vol 2, seals* (pp. 145–170). London: Academic.
- Burns, J. J. (1981b). Ribbon seal – *Phoca fasciata*. In S. H. Ridgeway & R. J. Harrison (Eds.), *Handbook of marine mammals. vol 2, seals* (pp. 89–109). London: Academic.
- Cárdenas-Alayza, S., Crespo, E., & Oliveira, L. 2016. *Otaria byronia*. The IUCN red list of threatened species 2016: e.T41665A61948292. Retrieved 22 Feb 2017, from <http://www.iucnredlist.org/details/41665/0>.
- Carrick, R., Csordas, S. E., Ingham, S. E., & Keith, K. (1962). Studies on the southern elephant seal, *Mirounga leonina* (L.). III. The annual cycle in relation to age and sex. *CSIRO Wildlife Research*, *7*(2), 119–160. doi:10.1071/CWR9620119.
- Chivers, B.L. (2015). *Phocarcetos hookeri*. The IUCN red list of threatened species 2015: e.T17026A1306343. Retrieved 22 Feb 2017, from <http://dx.doi.org/10.2305/IUCN.UK.2015-2.RLTS.T17026A1306343.en>.
- Cline, D. R., Siniff, D. B., & Erickson, A. W. (1971). Underwater copulation of the Weddell seal. *Journal of Mammalogy*, *52*, 216–218. doi:10.2307/1378453.
- Coltman, D. W., Bowen, W. D., Boness, D. J., & Iverson, S. J. (1997). Balancing foraging and reproduction in the male harbour seal, an aquatically mating pinniped. *Animal Behavior*, *54*, 663–678. doi:10.1006/anbe.1997.0470.
- Costa, D. P. (1991). Reproductive and foraging energetics of pinnipeds: Implications for life history patterns. In D. Renouf (Ed.), *The behavior of pinnipeds* (pp. 300–344). London: Chapman and Hall.
- Costa, D. P., & Gentry, R. L. (1986). Free-ranging energetics of northern fur seal. In R. L. Gentry and G. L. Kooyman (Eds.) *Fur Seals: Maternal Strategies on land and at sea*, pp. 79–101. Princeton, New Jersey: Princeton University Press.
- Crocker, D. E., Williams, J. D., Costa, D. P., & Le Boeuf, B. J. (2001). Maternal traits and reproductive effort in northern elephant seals. *Ecology*, *82*(12), 3541–3555. doi: 10.1890/0012-9658(2001)082[3541:MTAREI]2.0.CO;2.
- Dasmahapatra, K. K., Hoffman, J. I., & Amos, W. (2009). Pinniped phylogenetic relationships inferred using AFLP markers. *Heredity*, *103*(2), 168–177. doi:10.1038/hdy.2009.25.
- Davis, C. S., Stirling, I., Strobeck, C., & Coltman, D. W. (2008). Population structure of ice-breeding seals. *Molecular Ecology*, *17*(13), 3078–3094. doi:10.1111/j.1365-294X.2008.03819.x.
- Doidge, D. W., McCann T. S., Crossall, J. P. (1986) Attendance behaviour of Antarctic fur seals. In R. L. Gentry and G. L. Kooyman (Eds.) *Fur Seals: Maternal Strategies on Land and at Sea* (pp. 102–114). Princeton University Press, Princeton.
- Erdsack, N., Hanke, F. D., Dehnhardt, G., & Hanke, W. (2012). Control and amount of heat dissipation through thermal windows in harbor seals (*Phoca vitulina*).

- Journal of Thermal Biology*, 37(7), 537–544. doi:10.1016/j.jtherbio.2012.06.002.
- Fay, F. H. (1982). Ecology and biology of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. *USDI North Am Fauna Series*, 74, 1–279. doi:10.2307/1381268.
- Fedak, M. A., & Anderson, S. S. (1982). The energetics of lactation: Accurate measurements from a large wild animal, the grey seal (*Halichoerus grypus*). *Journal of Zoology*, 198, 473–479. doi:10.1111/jzo.1982.198.4.473.
- Ferguson, S. H., & Higdon, J. W. (2006). How seals divide up the world: Environment, life history, and conservation. *Oecologia*, 150(2), 318–329. doi:10.1007/s00442-006-0489-x.
- Franco-Trecu, V., Costa-Urrutia, P., Schramm, Y., Tassinio, B., & Inchausti, P. (2015). Tide line versus internal pools: Mating system and breeding success of South American sea lion males. *Behavioral Ecology and Sociobiology*, 69(12), 1985–1996. doi:10.1007/s00265-015-2010-1.
- Gales, N. J., Fraser, W. R., Costa, D. P., & Southwell, C. (2004). Do crabeater seals forage cooperatively? *Deep-Sea Research Part II, Topical Studies In Oceanography*, 51(17–19), 2305–2310. doi:10.1016/j.dsr2.2004.07.006.
- Gallo-Reynoso, J., & Figueroa-Carranza, A. (1996). Size and weight of Guadalupe fur seals. *Marine Mammal Science*, 12(2), 318–321.
- Giardino, G. V., Mandiola, M. A., Bastida, J., Denuncio, P. E., Bastida, R. O., & Rodríguez, D. H. (2016). Travel for sex: Long-range breeding dispersal and winter haulout fidelity in southern sea lion males. *Mammalian Biology*, 81(1), 89–95. doi:10.1016/j.mambio.2014.12.003.
- Goldsworthy, S. D. (2015). *Neophoca cinerea*. The IUCN red list of threatened species 2015: e.T14549A45228341. Retrieved 22 Feb 2017, from <http://dx.doi.org/10.2305/IUCN.UK.2015-2.RLTS.T14549A45228341.en>
- González-Suárez, M., & Cassini, M. H. (2014). Variance in male reproductive success and sexual size dimorphism in pinnipeds: Testing an assumption of sexual selection theory. *Mammal Review*, 44(2), 88–93. doi:10.1111/mam.12012.
- Hamilton, J. E. (1934). The Southern sea lion, *Otaria byronia* (de Blainville). *Discovery Reports*, 8, 269–318.
- Hammill, M. O., Lydersen, C., Ryg, M., & Smith, T. G. (1991). Lactation in the ringed seal (*Phoca hispida*). *Canadian Journal of Fisheries and Aquatic Sciences*, 48(12), 2471–2476. doi:10.1139/f91-288).
- Hanggi, E. B., & Schusterman, R. J. (1990). Kin recognition in captive California sea lions (*Zalophus californianus*). *Journal of Comparative Psychology*, 104(4), 368–372. doi:10.1037/0735-7036.104.4.368.
- Harcourt, R. G., Hindell, M. A., & Waas, J. R. (1998). Under ice movements and territory use in free-ranging Weddell seals during the breeding season. *New Zealand Natural Sciences*, 23, 72–73. doi:10.1017/S0954102014000297.
- Harcourt, R. G., Hindell, M. A., Bell, D. G., & Waas, J. R. (2000). Three-dimensional dive profiles of free-ranging Weddell seals. *Polar Biology*, 23, 479–487. doi:10.1007/s003000000109.
- Heerah, K., Hindell, M., Guinet, C., & Charrassin, J. (2014). A new method to quantify within dive foraging behaviour in marine predators. *PLoS One*, 9(6), 1–15. doi:10.1371/journal.pone.0099329.
- Higdon, J. W., Bininda-Emonds, O. P., Beck, R. D., & Ferguson, S. H. (2007). Phylogeny and divergence of the pinnipeds (Carnivora: Mammalia) assessed using a multigene dataset. *BMC Evolutionary Biology*, 7216–7234. doi:10.1186/1471-2148-7-216.
- Higdon, J. W., Bininda-Emonds, O. P., Beck, R. D., & Ferguson, S. H. (2008). Phylogeny and divergence of the pinnipeds (Carnivora: Mammalia) assessed using a multigene dataset. *BMC Evolutionary Biology*, 81–82. doi:10.1186/1471-2148-8-216.
- Hocking, D., Evans, A., & Fitzgerald, E. (2013). Leopard seals (*Hydrurga leptonyx*) use suction and filter feeding when hunting small prey underwater. *Polar Biology*, 36(2), 211–222. doi:10.1007/s00300-012-1253-9.
- Hoffman, J. I., & Forcada, J. (2009). Genetic analysis of twinning in Antarctic fur seals (*Arctocephalus gazella*). *Journal of Mammalogy*, 90(3), 621–628. doi:10.1644/08-MAMM-A-264R1.1.
- Hoffman, J. I., & Forcada, J. (2012). Extreme natal philopatry in female Antarctic fur seals (*Arctocephalus gazelle*). *Mammalian Biology*, 77, 71–73. doi:10.1016/j.mambio.2011.09.002.
- Hofmeyr, G. J. G. (2015a). *Mirounga leonina*. The IUCN red list of threatened species 2015: e.T13583A45227247. Retrieved 22 Feb 2017, from <http://dx.doi.org/10.2305/IUCN.UK.2015-4.RLTS.T13583A45227247.en>
- Hofmeyr, G. J. G. (2015b). *Arctocephalus tropicalis*. The IUCN red list of threatened species 2015: e.T2062A45224547. Retrieved 22 Feb 2017, from <http://dx.doi.org/10.2305/IUCN.UK.2015-4.RLTS.T2062A45224547.en>
- Insley, S. J. (2000). Long-term vocal recognition in the northern fur seal. *Nature*, 406(6794), 404–405. doi:10.1038/35019064.
- Insley, S. J., Phillips, A. V., & Charrier, I. (2003). A review of social recognition in pinnipeds. *Aquatic Mammals*, 29, 181–201.
- Karamanlidis, A., & Dendrinou, P. (2015). *Monachus monachus*. The IUCN red list of threatened species 2015: e.T13653A45227543. Retrieved 22 Feb 2017, from <http://dx.doi.org/10.2305/IUCN.UK.2015-4.RLTS.T13653A45227543.en>
- Kastelein, R. A., van den Belt, I., Jennings, N., & de Kuijff, R. (2014). Behavior and body mass changes of a mother and calf Pacific walrus (*Odobenus rosmarus divergens*) during the suckling period. *Zoo Biology*, 24(1), 9–19. doi:10.1002/zoo.21189

- Kaufman, G. W., Siniff, D. B., & Reichle, R. (1975). Colony behavior of Weddell seals, *Leptonychotes weddelli* at Hutton Cliffs, Antarctica. *Rapports et procès verbaux des réunions – Commission internationale pour l'exploration scientifique de la mer Méditerranée*, 169, 228–246.
- Kerley, G. I. H. (1985). Pup growth in the fur seals *Arctocephalus tropicalis* and *A. gazella* on Marion Island. *Journal of Zoology*, 205(3), 315–324. doi: 10.1111/j.1469-7998.1985.tb05619.x
- Kiyota, M., & Okamura, H. (2005). Harassment, abduction, and mortality of pups by nonterritorial male northern fur seals. *Journal of Mammalogy*, 85(6), 1227–1236. doi:10.1644/04-MAMM-A-031R2.1.
- Koretsky, I. A., & Barnes, L. G. (2003). Origins and relationships of pinnipeds, and the concepts of monophyly versus diphyly. *Journal of Vertebrate Paleontology*, 23, 69A.
- Koretsky, I. A., & Holec, P. (2002). A primitive seal (Mammalia: Phocidae) from the early middle Miocene of central Paratethys. *Smithsonian Contributions to Paleobiology*, 93, 163–178.
- Koretsky, I. A., & Sanders, A. (2002). Paleontology of the late oligocene ashley and chandler bridge formations of South Carolina, 1: Paleogene pinniped remains; the oldest known seal (Carnivora: Phocidae). *Smithsonian Contributions to Paleobiology*, 93, 179–184.
- Koretsky, I. A., Barnes, L. G., & Rahmat, S. J. (2016). Re-evaluation of morphological characters questions current views of pinniped origins. *Vestnik Zoologii*, 50(4), 327–354. doi:10.1515/vzoo-2016-0040.
- Kovacs, K. M., & Lavigne, D. M. (1986). Growth of grey seal (*Halichoerus grypus*) neonates: Differential maternal investment in the sexes. *Canadian Journal of Zoology*, 64(9), 1937–1943. doi:10.1139/z86-291.
- Kovacs, K. M., & Lavigne, D. M. (1992). Mass transfer efficiency between hooded seal (*Cystophora cristata*) mothers and their pups in the Gulf of St. Lawrence. *Canadian Journal of Zoology*, 70, 1315–1320. doi:10.1139/z92-184.
- Le Boeuf, B. J. (1981). Elephant seals. In B. J. LeBoeuf & S. Kaza (Eds.), *The natural history of Ano Nuevo* (pp. 326–374). Pacific Grove: Boxwood Press.
- Ling, J. K. (1970). Pelage and molting in wild animals with special reference to aquatic forms. *Quarterly Review of Biology*, 45, 16–54. doi:10.1086/406361.
- Ling, J. K., & Walker, G. E. (1976). Seal studies in South Australia: Progress report for the year 1975. *South Australian Naturalist*, 50, 59–68.
- Littnan, C., Harting, A. & Baker, J. (2015). *Neomonachus schauinslandi*. The IUCN Red List of Threatened Species 2015: e.T13654A45227978. Retrieved on February 22, 2017 from <http://dx.doi.org/10.2305/IUCN.UK.2015-2.RLTS.T13654A45227978.en>.
- Longstreth, C. (2016). The northern elephant seal. *Natural History*, 124(1), 14–19.
- Lowenstein, J. (1986). The pinniped family tree puzzle. *Oceans*, 19(2), 72.
- Lowry, L. (2016). *Odobenus rosmarus*. The IUCN red list of threatened species 2016: e.T15106A45228501. Retrieved 22 Feb 2017, from <http://dx.doi.org/10.2305/IUCN.UK.2016-1.RLTS.T15106A45228501.en>
- Luschi, P. (2013). Long-distance animal migrations in the oceanic environment: Orientation and navigation correlates. *ISRN Zoology*, 1–23. doi:10.1155/2013/631839.
- Marlow, B. J. (1975). The comparative behaviour of the Australasian sea lions *Neophoca cinerea* and *Phocarctos hookeri* (pinnipedia: otariidae). *Mammalia*, 39(2), 159–230. doi <https://doi.org/10.1515/mamm.1975.39.2.159>
- Mauck, B., Gläser, N., Schlosser, W., & Dehnhardt, G. (2008). Harbour seals (*Phoca vitulina*) can steer by the stars. *Animal Cognition*, 11(4), 715–718. doi:10.1007/s10071-008-0156-1.
- McLaren, I. A. (1958). The biology of the ringed seal (*Phoca greonlandica* Schreber) on the eastern Canadian Arctic. *Bulletin of the Fisheries Research Board of Canada*, 118, 1–97.
- Modig, A. O. (1996). Effects of body size and harem size on male reproductive behaviour in the southern elephant seal. *Animal Behaviour*, 51(6), 1295–1306. doi:10.1006/anbe.1996.0134.
- National Oceanic and Atmospheric Administration (NOAA). (2015). Marine Mammal Stock Assessment Reports (SARs) by Species/Stock: Hawaiian Monk Seal. Retrieved 21 Feb 2017, from [http://www.fisheries.noaa.gov/pr/sars/pdf/stocks/pacific/2015/monkseal-hi\\_2015.pdf](http://www.fisheries.noaa.gov/pr/sars/pdf/stocks/pacific/2015/monkseal-hi_2015.pdf)
- National Oceanic and Atmospheric Administration (NOAA). (2016). Guadalupe Fur Seal (*Arctocephalus townsendi*). Retrieved on February 21, 2017 from <http://www.nmfs.noaa.gov/pr/species/mammals/seals/guadalupe-fur-seal.html>
- Nomokonova, T., Losey, R. J., Iakunaeva, V. N., Emel'ianova, I. A., Baginova, E. A., & Pastukhov, M. V. (2013). People and seals at Siberia's Lake Baikal. *Journal of Ethnobiology*, 33(2), 259–280. doi:10.2993/0278-0771-33.2.259.
- Oftedal, O. T., Bowen, W. D., & Boness, D. J. (1993). Lactation performance and nutrient deposition in pups of the harp seal, *Phoca groenlandica*, on ice floes off southeast Labrador. *Physiological Zoology*, 69, 635–657. <http://www.jstor.org/stable/30164220>.
- Pastukhov, V. D. 1990. Biological features of sustainable use and conservation of Baikal seal. [Biologicheskije osnovy ispol'zovaniya i okhrany resursov baykal'skoy nerpy]. Avtoref. dis. dokt. biol. nauk. M.
- Pastukhov, V. D. (1993). *Baikal seal Nerpa Baikala: Biologicheskije Osnovy Ratzional'nogo Ispol'zovaniia i Okhrana Resursov*. Novosibirsk: Nauka.
- Payne, M. R., (1979). Growth in the Antarctic fur seal *Arctocephalus gazelle*. *Journal of Zoology*, 187(1), 1–20. doi: 10.1111/j.1469-7998.1979.tb07709.x
- Peterson, R. S. (1965). Behavior of northern fur seal. *American Zoologist*, 5(2), 217.

- Pomeroy, P. (2011). Reproductive cycles in marine mammals. *Animal Reproductive Science*, 124, 184–193. doi:10.1016/j.anireprosci.2010.08.021sealsoeuf.
- Porter, B. T., & Trites, A. W. (2004). Suckling attempts during winter by two non-filial Steller sea lion pups (*Eumetopias jubatus*). *Mammalia*, 68, 23–26. doi:10.1515/mamm.2004.003.
- Reiter, J., Stinson, N. L., & Le Boeuf, B. J. (1978). Northern elephant seal development: The transition from weaning to nutritional independence. *Behavioral Ecology and Sociobiology*, 3, 337–367. doi:10.1007/BF00303199.
- Reiter, J., Panken, K. J., & Le Boeuf, B. J. (1981). Female competition and reproductive success in northern elephant seals. *Animal Behavior*, 29, 670–687. doi:10.1016/S0003-3472(81)80002-4.
- Repenning, C. A. (1976). Adaptive evolution of the sea lions and walruses. *Systematic Zoology*, 25, 375–390. doi:10.2307/2412512.
- Riedman, M. (1990). *The pinnipeds: Seals, sea lions, and walruses*. Berkeley: University of California Press.
- Ronald, K., & Healey, P.J. (1981). Harp seal - *Phoca groenlandica*. In S.h. Ridgeway and R. J. Harrison (Eds.) *Handbook of Marine Mammals, Volume 2. Seals* (pp.55–87). London: Academic Press.
- Roux, J. P., & Hess, A. D. (1984). The seasonal haul-out of the fur seal, *Arctocephalus tropicalis* (gray 1872) on Amsterdam Island. *Mammalia*, 48, 377–389. doi:10.1515/mamm.1984.48.3.377.
- Schultz, J. K., Becker, B. L., Johanos, T. C., Lopez, J. U., & Kashinsky, L. (2011). Dizygotic twinning in the Hawaiian monk seal. *Journal of Mammology*, 92(2), 336–341. doi:10.1644/10-MAMM-A-275.1.
- Schulz, T. M., & Bowen, W. D. (2005). The evolution of lactation strategies. In pinnipeds: A phylogenetic analysis. *Ecological Monographs*, 75(2), 159–177. doi:10.1890/04-0319.
- Schusterman, R. J., Kastak, C. R., & Kastak, D. (2002). The cognitive sea lion: Meaning and memory in the laboratory and in nature. In M. Bekoff, C. Allen, G. M. Burghardt, M. Bekoff, C. Allen, & G. M. Burghardt (Eds.), *The cognitive animal: Empirical and theoretical perspectives on animal cognition* (pp. 217–228). Cambridge, MA: MIT Press.
- Shero, M. R., Krotz, R. T., Costa, D. P., Avery, J. P., & Burns, J. M. (2015). How do overwinter changes in body condition and hormone profiles influence Weddell seal reproductive success? *Functional Ecology*, 29(10), 1278–1291. doi:10.1111/1365-2435.12434.
- Stephens, P. P., Houston, A. I., Harding, K. C., Boyd, I. L., & McNamara, J. M. (2014). Capital and income breeding: The role of food supply. *Ecology*, 95(4), 882–896. doi:10.1890/13-1434.1.
- Stewarts, B. S., & Yochem, P. (1984). Seasonal abundance of pinnipeds at San Nicolas Island, California, 1980–1982. *Bulletin of the Southern California Academy of Sciences*, 83, 121–132. <http://scholar.oxy.edu/scas/vol83/iss3/7>
- Trillmich, F. (1979). Galapagos sea lions and fur seals. *Noticias de Galapagos*, 29, 8-14.
- Trillmich, F., & Lechner, E. (1986). Milk of the Galapagos fur seal and sea lion, with a comparison of the milk of eared seals (Otariidae). *Journal of Zoology*, 209, 271–277.
- Trimble, M., & Insley, S. J. (2010). Mother-offspring reunion in the South American sea lion *Otaria flavescens* at Isla de lobos (Uruguay): Use of spatial, acoustic and olfactory cues. *Ethology Ecology and Evolution*, 22(3), 233–246. doi:10.1080/03949370.2010.502318.
- United States Fish and Wildlife (USFW). 2016. *Threatened and endangered species*. Retrieved from <https://www.fws.gov/endangered/> on February 7, 2017.
- United States Fish and Wildlife (USFW). 2017. Threatened and endangered species. Retrieved 7 Feb 2017, from <http://ecos.fws.gov/ecp/>
- Van Parijs, S. M. (2003). Aquatic mating in pinnipeds: A review. *Aquatic Mammals*, 29(2), 214–226. doi:10.1578/016754203101024167.
- Vaz-Ferreira, R. & Ponce de Leon, A. (1987). South American fur seal, *Arctocephalus australis*, in Uruguay. In J. P. Croxall and R. L. Gentry (Eds.) *Status, Biology, and Ecology of fur seals. Proceeding of an International Symposium and Workshop*. Cambridge, England April 23–27, 1984.
- Zhang, P. J., Song, X. R., Han, J. B., Wang, L. M., & Yang, Y. (2014). Milk composition, milk consumption, and growth rate of a captive spotted seal (*Phoca largha*) pup from Liaodong Bay, China. *Canadian Journal of Zoology*, 92, 449–452. doi:10.1139/cjz-2013-0295.

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## Jonathon Crystal

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### Introduction

The objective of work in the laboratory of Jonathon Crystal is to develop animal models of memory, focusing on the types of memory that are impaired in human diseases. This work involves development of a range of models to evaluate elements of human memory in animals. For example, a number of techniques for evaluating cognition in rats have been developed, including binding of episodic memories (Crystal and Smith 2014), prospective memory (Wilson et al. 2013), what-where-when memory (Babb and Crystal 2006; Zhou and Crystal 2009), source memory (Crystal et al. 2013a), and retrieval practice (Crystal et al. 2013b). These models can be applied to translational models of human diseases of memory, such as Alzheimer's disease.

### Biographical Information and Career History

Crystal was born and raised in Toronto, Ontario. He was an undergraduate at the University of Toronto, where he was fortunate to have two

outstanding mentors, Ken Cheng and Sara J. Shettleworth. He spent almost 3 years in Ken's lab and a year in Sara's lab. He was also fortunate to publish articles with Ken (in 1993 in the *Journal of Experimental Psychology: Animal Behavior Processes*) and Sara (in 1994 in *Animal Learning & Behavior*), based on research he conducted as an undergraduate (including an honor's thesis conducted in Sara's lab). The Natural Sciences and Engineering Research Council of Canada (NSERC) provided Undergraduate Research Awards, which allowed him to spend three summers in the lab at "1 Spadina" (where Ken and Sara had their labs). The environment at 1 Spadina was outstanding for animal behavior and cognition (in addition to Ken and Sara, others included Jerry Hogan, David Sherry, and their grad students). Dave Brodbeck and Rob Hampton (grad students at 1 Spadina) were particularly influential for Crystal. Crystal received a Bachelor of Science degree from Toronto in 1992.

Crystal became interested in time perception from immersion in Ken's lab and courses offered by Sara and Ken. This interest led Crystal to attend Brown University for grad school and to work in the laboratory of Russell M. Church beginning in 1992. Crystal was fortunate to have Russ as an outstanding mentor in science, academics, and life. At Brown, Crystal focused on testing the hypothesis that timing is based on multiple endogenous oscillators. Crystal received 4 years of support from NSERC as a 1967 Science and Engineering Scholar at Brown. At Brown, he



met his future wife, Andrea Hohmann, who was also a grad student in psychology. They were married in Providence RI in 1997. Crystal received from Brown a Master's of Science in 1994 and a PhD in 1997. Part of Crystal's dissertation research was recognized by the New Investigator Research Award in Experimental Psychology (in 2000, from the American Psychological Association, Division 3).

In 1997, Crystal became an assistant professor of psychology at the College of William & Mary. In 1999, Crystal moved to the University of Georgia, where he and Andrea both took positions as assistant professors of psychology. In 2004, Crystal was promoted to associate professor, and in 2009 he was promoted to full professor. In 2010, Crystal and Hohmann moved to Indiana University, Department of Psychological & Brain Sciences. Other affiliations at Indiana University include the Program in Neuroscience, the Cognitive Science Program, and the Center for the Integrative Study of Animal Behavior. In 2013, Crystal became the Director of the Program in Neuroscience, a position that ends in 2018.

Crystal has served in a number of editorial roles. In 2016, Crystal became the Editor-in-Chief of *Learning & Behavior*, a position that ends in 2019. Earlier, he served as an Associate Editor of *Learning & Behavior* (2007–2015) and an Associate Editor of *Behavioural Processes* (2003–2007). Service on editorial boards include *Animal Cognition*, *Journal of Experimental Psychology: Animal Learning and Cognition*, *International Journal of Comparative Psychology*, *Comparative Cognition & Behavior Reviews*, and *Behavioural Processes*. Crystal was fortunate to serve as the Guest Editor of special issues of *Behavioral Processes* in honor of Russ Church (in 2007) and Tony Wright (in 2010, co-edited with Jeff Katz).

Crystal has also served in a number of leadership positions. In 2017, he serves as the President of the Society for Experimental Psychology and Cognitive Science (Division 3 of the American Psychological Association, a position that ends in 2018). He has a long-standing connection to the Comparative Cognition Society (President: 2010–2012. Secretary: 2006–2010. Executive

committee member: since 2006. A founding member in 1999).

Crystal is a Fellow of the American Psychological Association (Division 3 in 2006 and Division 6 in 2011), the Association of Psychological Science (2007), the Psychonomic Society (2014), and the Eastern Psychological Association (2013).

## Contributions to Science

Crystal has made a number of contributions to science, as outlined below. A complete list of publications can be found at the National Library of Medicine:

<http://www.ncbi.nlm.nih.gov/sites/myncbi/jonathon.crystal.1/bibliography/40423670/public/?sort=date&direction=ascending>

## Animal Model of What-Where-when Memory

The Crystal lab developed and validated a rodent model of what-where-when memory. The field of research into episodic memory in nonhumans began with a prominent paper in *Nature* by Nicky Clayton and Tony Dickinson (using food-storing scrub jays) in 1998. Although a number of labs were initially unable to develop an analogue using other species (papers in 2002–2005), the Crystal lab developed a working model in rats (Babb and Crystal 2005, 2006). A major alternative to episodic memory (focusing on judgments of relative familiarity) was published in *Science* by Bill Roberts in 2008. The Crystal lab developed an approach to eliminate the relative familiarity alternative explanation, which was published in *PNAS* (Zhou and Crystal 2009). Subsequent work has used this later approach to the problem of familiarity. Although the question of episodic memory in nonhumans was initially controversial, this body of work is now widely accepted. The approach taken by the Crystal lab focuses on the content of episodic memory, not on any subjective experiences that are thought to accompany episodic memory in people.



## Animal Model of Source Memory

The Crystal lab developed the first evidence of source memory in a nonhuman (Crystal et al. 2013a). Source memory refers to memories about the conditions under which information was acquired. Episodic memory typically involves source memory because those memories focus on the origin of representations. Importantly, source memory allows us to differentiate one episodic memory from another because source memory includes features that were present when the memory was formed. This model has been validated and used to demonstrate that episodic memories are bound by the source features encoded with the episode (Crystal and Smith 2014).

## Animal Model of Prospective Memory

The Crystal lab developed the first evidence for prospective memory in a nonhuman (Wilson and Crystal 2012; Wilson et al. 2013). Prospective memory is the ability to remember to take some action in the future. Failure of prospective memory is a common feature of aging and negatively impacts both health and independence. Currently, the only other working model of prospective memory in nonhumans comes from research with nonhuman primates.

## Other Models of Memory

The Crystal lab developed a number of other animal models of memory. These models are integrative as research seeks to identify the elements of human memory that can be modeled in nonhumans. Compelling evidence for episodic memory in nonhumans comes from the demonstration that rats can answer an unexpected question after incidentally encoding information, an ability that requires a functioning hippocampus (Zhou et al. 2012). The Crystal lab showed that rats use episodic memory to remember multiple events (at least 30 items in context; Panoz-Brown et al. 2016). The Crystal lab also developed the first

evidence for retrieval practice in a nonhuman (Crystal et al. 2013b) and independent working memory buffers (Bratch et al. 2016). Previously, the Crystal lab developed methods to assess meta-cognition in rats (Foote and Crystal 2007).

## Contributions to Timing Literature

Crystal's early work focused on testing the hypothesis that timing is based on multiple endogenous oscillators. This work integrated approaches from chronobiology with techniques from interval timing. This research program provided evidence that short-interval timing is based on endogenous oscillators with short periods (extending the reach of chronobiology) and that long intervals (below the limited range of circadian entrainment) can be timed (extending the reach of scalar timing into the range of hours, e.g., 3–16 h) (Crystal 2012).

## Collaborators

In addition to the influence of mentors (Cheng, Shettleworth, and Church), Crystal has been fortunate to have a range of other collaborators. He has benefited from talented graduate students (Matt Pizzo, Stephanie Babb, Allison Foote, Wenyi Zhou, George Wilson, Xan Smith, and Danielle Panoz-Brown) and undergrads (Aaron Ketzenberger, Xan Smith, Stefan Dalecki, and Alex Bratch). His lab has benefited from a small army of undergrads who have enabled the lab to explore memory using olfactory stimuli, many of whom are coauthors on papers from the lab (Bratch et al. 2016; Panoz-Brown et al. 2016). Collaborators at the University of Georgia include Ruth Furukawa, Marcus Fechheimer, and John Wagner, who provided opportunities to explore cognition in transgenic mouse models of Alzheimer's disease. Frequent collaborations with the Hohmann lab have opened outstanding new opportunities too numerous to list.

## Cross-References

- ▶ [Biological Rhythms](#)
- ▶ [Circadian Rhythms](#)
- ▶ [Comparative Cognition](#)
- ▶ [Endogenous Oscillations](#)
- ▶ [Episodic Memory](#)
- ▶ [Interval Clock](#)
- ▶ [Interval Timing](#)
- ▶ [Ken Cheng](#)
- ▶ [Memory](#)
- ▶ [Meta-Cognition](#)
- ▶ [Prospective Memory](#)
- ▶ [Russell Church](#)
- ▶ [Sara Shettleworth](#)
- ▶ [Scalar Timing Theory](#)
- ▶ [Timing](#)
- ▶ [Weber's law](#)
- ▶ [Working Memory](#)

## References

- Babb, S. J., & Crystal, J. D. (2005). Discrimination of what, when, and where: Implications for episodic-like memory in rats. *Learning & Motivation, 36*, 177–189. doi:[10.1016/j.lmot.2005.02.009](#).
- Babb, S. J., & Crystal, J. D. (2006). Episodic-like memory in the rat. *Current Biology, 16*, 1317–1321. doi:[10.1016/j.cub.2006.05.025](#).
- Bratch, A., Kann, S., Cain, J. A., Wu, J.-E., Rivera-Reyes, N., Dalecki, S., Arman, D., Dunn, A., Cooper, S., Corbin, H. E., Doyle, A. R., Pizzo, M. J., Smith, A. E., & Crystal, J. D. (2016). Working memory systems in the rat. *Current Biology, 26*(3), 351–355. doi:[10.1016/j.cub.2015.11.068](#).
- Crystal, J. D. (2012). Sensitivity to time: Implications for the representation of time. In E. A. Wasserman & T. R. Zentall (Eds.), *The Oxford handbook of comparative cognition* (pp. 434–450). New York: Oxford University Press.
- Crystal, J. D., Alford, W. T., Zhou, W., & Hohmann, A. G. (2013a). Source memory in the rat. *Current Biology, 23*(5), 387–391. doi:[10.1016/j.cub.2013.01.023](#).
- Crystal, J. D., Ketzenberger, J. A., & Alford, W. T. (2013b). Practicing memory retrieval improves long-term retention in rats. *Current Biology, 23*(17), R708–R709. doi:[10.1016/j.cub.2013.07.044](#).
- Crystal, J. D., & Smith, A. E. (2014). Binding of episodic memories in the rat. *Current Biology, 24*(24), 2957–2961. doi:[10.1016/j.cub.2014.10.074](#).
- Foote, A. L., & Crystal, J. D. (2007). Metacognition in the rat. *Current Biology, 17*(6), 551–555. doi:[10.1016/j.cub.2007.01.061](#).
- Panoz-Brown, D. E., Corbin, H. E., Dalecki, S. J., Gentry, M., Brotheridge, S., Sluka, C. M., Wu, J.-E., & Crystal, J. D. (2016). Rats remember items in context using episodic memory. *Current Biology, 26*(20), 2821–2826. doi:[10.1016/j.cub.2016.08.023](#).
- Wilson, A. G., & Crystal, J. D. (2012). Prospective memory in the rat. *Animal Cognition, 15*(3), 349–358. doi:[10.1007/s10071-011-0459-5](#).
- Wilson, A. G., Pizzo, M. J., & Crystal, J. D. (2013). Event-based prospective memory in the rat. *Current Biology, 23*(12), 1089–1093. doi:[10.1016/j.cub.2013.04.067](#).
- Zhou, W., & Crystal, J. D. (2009). Evidence for remembering when events occurred in a rodent model of episodic memory. *Proceedings of the National Academy of Sciences of the United States of America, 106*(23), 9525–9529. doi:[10.1073/pnas.0904360106](#).
- Zhou, W., Hohmann, A. G., & Crystal, J. D. (2012). Rats answer an unexpected question after incidental encoding. *Current Biology, 22*(12), 1149–1153. doi:[10.1016/j.cub.2012.04.040](#).

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# M

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## Michael J. Beran

Michael J. Beran  
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have done for him. He tries every day to pay that forward through work with his own students and other students who he works with. In his career, he is most proud of who those students have become.

### Early Life and Educational Background

Beran was born to Ellen L. and Robert A. Beran on August 11, 1973, in Middlefield, OH, but he grew up in Birmingham, AL, with one brother, Matthew. He received his B.A. in Psychology from Oglethorpe University in 1995, after some time as an accounting major, a business major, and a political science major (as well as at least one semester where he was undeclared!). Apparently what was required was the time needed to take courses in cognitive psychology and animal learning, and the realization that people could study both. He discovered this and his broader enjoyment of psychology because of the guidance of three faculty members, Nancy Kerr, Timothy Hand, and Adrian Brock. He received his M.A. (1997) and Ph.D. (2002) in the Department of Psychology at Georgia State University. His dissertation research focused on mathematical operations by chimpanzees and was conducted under the supervision of David A. Washburn, who he also routinely defeated at racquetball, basketball, and ping-pong, or at least that is how he remembers things. Additional mentors during his graduate career were Duane Rumbaugh and James Pate, and he is grateful to these three people for all they

### Professional Career

Beran took a research staff position at Georgia State University during the latter part of his graduate training, with support from NICHD and support as the inaugural Duane M. Rumbaugh Fellow at Georgia State. He has remained at Georgia State University throughout his career, although he also spent time as a Visiting Lecturer at Spelman College from 2003 to 2007. He was a Research Associate and then Senior Research Associate at the Language Research Center of Georgia State before joining the Psychology Department at GSU as Associate Professor in 2015. He has authored more than 250 publications during his career including more than 150 peer-reviewed journal articles, which have appeared in outlets such as *Proceedings of the National Academy of Sciences*, *Psychological Science*, *Current Directions in Psychological Science*, *Current Biology*, *Journal of Experimental Psychology: General*, *Journal of Experimental Psychology: Animal Behavior Processes*, *Journal of Comparative Psychology*, *Animal Cognition*, and *Animal Behaviour*.

Beran has received several awards and recognitions. He is a Fellow of the American

Psychological Association (APA Division 3 and Division 6) and the Psychonomics Society. He served as the President of the Southern Society of Philosophy and Psychology (SSPP), as well as serving as the Treasurer of that organization. He has served on the Executive Councils of the Southeastern Psychological Association and Division 3 and Division 6 of the APA, and he has been elected as President of the Southeastern Psychological Association. He received the Brenda A. Milner Award from the APA and the Richard M. Griffith Memorial Award from the SSPP.

Beran serves as the current co-editor of *Animal Behavior and Cognition* and is on the editorial boards of *Cognition*, *Frontiers in Comparative Psychology*, *Journal of Comparative Psychology*, *Comparative Cognition & Behavior Reviews*, *Learning & Behavior*, *Journal of Experimental Psychology: Animal Learning and Cognition*, *Animal Cognition*, and the *International Journal of Comparative Psychology*. His research has been supported by grants from the National Science Foundation, the National Institute of Child Health and Human Development, the European Science Foundation, and the Templeton Foundation.

## Research Interests

Beran and his students and collaborators focus on comparative cognition with an emphasis on nonhuman primates, particularly chimpanzees, capuchin monkeys, and rhesus monkeys, and human children and adults (Beran 2015; Beran and Heimbauer 2015; Beran et al. 2015a, 2016; Heimbauer, Beran, and Owren 2011). They sometimes work with other species, such as elephants, bears, gorillas, and orangutans.

Beran has assessed counting and arithmetic skills in nonhuman primates, human adults, and human children. His research has contributed to the notion that other species share with human an Approximate Number System (ANS), in which quantitative information including the numbers of items in sets can be encoded and represented,

but with a degree of increasing inexactness as a function of true size, amount, or number (e.g., Beran 2001, 2007; Beran and Beran 2004; Beran and Parrish 2016). Among the many things that chimpanzees and monkeys have shown is that they can learn the values of Arabic numerals. They also can compare sets of items on the basis of numerosity, even when items are presented one at a time and the whole set can never be seen at once, and even when they have to compare auditory sets (hearing dropped items) compared to static visual sets (seeing all items at once). Sometimes, however, they show perceptual illusions about size similar to those seen in humans (Parrish and Beran 2014).

Beran also has made contributions to the study of metacognition in nonhuman animals (Beran, Brandl, Perner, and Proust 2012). Here, the question is whether animals may experience some sense of knowing what they do or do not know when faced with a decision. This is a difficult thing to assess in animals given the role of verbal reports in our understanding of human metacognition. However, certain experimental procedures have provided insights into the metacognitive skills of nonhuman animals (e.g., Beran and Smith 2011). For example, monkeys can be presented with various psychophysical and memory tasks for which stimuli can be categorized objectively as more difficult or less difficult for the animals based on task performance. Animals also are given an additional response option, called the uncertainty response, that allows the animals to “escape” from choices that are too difficult or error-risking. In many cases, the animals use that response on exactly those trials for which the primary response is made least efficiently. This suggests that animals may monitor their own knowledge states when faced with decisions about how to respond to stimuli. Beran has focused particularly on chimpanzee metacognition (e.g., Beran, Smith, and Perdue 2013), demonstrating that these animals seek information based on what they know (or do not know), and they also provide measures of confidence in their own memory abilities. They do this by

anticipating food reward for correct responses even before any external feedback is given to them – in essence by responding as if they know they are going to be correct or are not sure about that (Beran et al. 2015b).

Beran has studied future-oriented cognitive processes in animals and children. The ability to flexibly plan for the future has long been reserved for humans, and some have argued that animals are “stuck in time,” and they cannot think about the past or future because their behavior is affected only by their current needs and surroundings. However, animals may show capacities for mental time travel. Beran and his students and colleagues test nonhuman primates’ ability to anticipate future situations and plan future actions so as to determine continuities and discontinuities in the prospective memory and planning abilities of humans and other primates. This research has shown that nonhuman animals do have prospective memories and can anticipate future needs and remember to make responses in the future (e.g., Beran, Evans, Klein, Einstein 2012).

Beran also has spent his career learning about how nonhuman primates demonstrate self-control by delaying gratification. Delay of gratification occurs when one chooses to wait for something bigger or better rather than taking something that is available more immediately. Beran devised a way to use with nonhuman primates a task originally presented to children. In this task, animals learn that food items continue to pile up before them as long as they do not eat any. Thus, the longer they wait, the more they get by delaying gratification. This simple technique has provided compelling evidence that chimpanzees show excellent delay of gratification (sometimes for periods in excess of 20 minutes with highly preferred food accumulating in front of them). Even rhesus monkeys and capuchin monkeys, traditionally viewed as more impulsive species, show some success with this task. Beran and his colleagues also have shown that chimpanzees can even use self-distraction to help aid delay of gratification (Evans and Beran 2007).

Ultimately, the “lab culture” that Beran tries to instill in these and other research programs is inspired by this quote from Edward Tolman in

1959 – “Since all the sciences, and especially psychology, are still immersed in such tremendous realms of the uncertain and the unknown, the best that any individual scientist, especially any psychologist, can do seems to be to follow his own gleam and his own bent, however inadequate they may be. In fact, I suppose that actually this is what we all do. In the end, the only sure criterion is to have fun.”

## Cross-References

- ▶ [Addition](#)
- ▶ [Approximate Number System](#)
- ▶ [Arabic numerals](#)
- ▶ [David Washburn](#)
- ▶ [Duane Rumbaugh](#)
- ▶ [Georgia State Language Research Center](#)
- ▶ [Sarah, Lana, Sherman & Austin \(chimpanzees\)](#)

## References

- Beran, M. J. (2001). Summation and numerosness judgments of sequentially presented sets of items by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, 115, 181–191.
- Beran, M. J., & Beran, M. M. (2004). Chimpanzees remember the results of one-by-one addition of food items to sets over extended time periods. *Psychological Science*, 15, 94–99.
- Beran, M. J. (2007). Rhesus monkeys (*Macaca mulatta*) enumerate large and small sequentially presented sets of items using analog numerical representations. *Journal of Experimental Psychology: Animal Behavior Processes*, 33, 42–54.
- Beran, M. J. (2015). Chimpanzee cognitive control. *Current Directions in Psychological Science*, 24, 352–357.
- Beran, M. J., & Heimbauer, L. A. (2015). A longitudinal assessment of vocabulary retention in symbol-competent chimpanzees (*Pan troglodytes*). *PLoS One*, 10, e0118408.
- Beran, M. J., & Parrish, A. E. (2016). Capuchin monkeys (*Cebus apella*) treat small and large numbers of items similarly during a relative quantity judgment task. *Psychonomic Bulletin & Review*, 23, 1206–1213.
- Beran, M. J., & Smith, J. D. (2011). Information seeking by rhesus monkeys (*Macaca mulatta*) and capuchin monkeys (*Cebus apella*). *Cognition*, 120, 90–105.
- Beran, M. J., Brandl, J., Perner, J., & Proust, J. (Eds.). (2012a). *Foundations of metacognition*. Oxford: Oxford University Press.

- Beran, M. J., Evans, T. A., Klein, E. D., & Einstein, G. O. (2012b). Rhesus monkeys (*Macaca mulatta*) and capuchin monkeys (*Cebus apella*) remember future responses in a computerized task. *Journal of Experimental Psychology: Animal Behavior Processes*, *38*, 233–243.
- Beran, M. J., Smith, J. D., & Perdue, B. M. (2013). Language-trained chimpanzees name what they have seen, but look first at what they have not seen. *Psychological Science*, *24*, 660–666.
- Beran, M. J., Perdue, B. M., Futch, S. E., Smith, J. D., Evans, T. A., & Parrish, A. E. (2015a). Go when you know: Chimpanzees' confidence movements reflect their responses in a computerized memory task. *Cognition*, *142*, 236–246.
- Beran, M. J., Parrish, A. E., Futch, S. E., Evans, T. A., & Perdue, B. M. (2015b). Looking ahead? Computerized maze task performance by chimpanzees (*Pan troglodytes*), rhesus monkeys (*Macaca mulatta*), capuchin monkeys (*Cebus apella*), and human children (*Homo sapiens*). *Journal of Comparative Psychology*, *129*, 160–173.
- Beran, M. J., Menzel, C. R., Parrish, A. E., Perdue, B. M., Sayers, K., Smith, J. D., & Washburn, J. D. (2016). Primate cognition: Attention, episodic memory, prospective memory, self-control, and metacognition as examples of cognitive control in nonhuman primates. *WIREs Cognitive Science*. doi:10.1002/wcs.1397.
- Evans, T. A., & Beran, M. J. (2007). Chimpanzees use self-distraction to cope with impulsivity. *Biology Letters*, *3*, 599–602.
- Heimbauer, L. A., Beran, M. J., & Owren, M. J. (2011). A chimpanzee recognizes synthetic speech with significantly reduced acoustic cues to phonetic content. *Current Biology*, *21*, 1210–1214.
- Parrish, A. E., & Beran, M. J. (2014). When less is more: Like humans, chimpanzees (*Pan troglodytes*) misperceive food amounts based on plate size. *Animal Cognition*, *17*, 427–434.

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# F

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## Frans de Waal

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Contemporary students of animal cognition move fluidly through doorways to fascinating capabilities – peacemaking, justice, fairness, morality, and empathy – to name just a few. So unimpeded is their progress that few may fully realize how briefly these doors have been open. They may not fully realize how much work and courage it took to systematically *wedge those doors open* with one persuasive discovery after another over the last few short decades.

The world of animal cognition we enjoy today, which this encyclopedia showcases so well, was unimaginable not long ago. For example, this author did her PhD under Frans de Waal on the development of reconciliation – studying how capuchin monkeys learn to apologize as youngsters. Capuchins were a good model because they grow up faster and are not quite as conscious of being studied as are apes and humans. During the final defense, this author was repeatedly questioned by a committee member about the role of personality in the capuchins' peacemaking behavior. "But we don't talk about personality in monkeys!" was her startled defense, as she cast entreating glances to Frans to help her out. The

questioning committee member was a human psychologist. He was incredulous that animal behaviorists dared not invoke personality or emotion in the animals we studied (if they wished to avoid professional crucifixion). Denying things like personality and emotions was very hard and always awkward. Yet that denial was still largely the tenor of the time. Where did the invisible wall that completely blocked legitimate investigation of fascinating possibilities of animal cognition come from?

There is little question where it came from. René Descartes was wrong when he claimed that animals were stupid machines – organic automata without thoughts or feelings. But that did not stop three centuries of people from believing him. Descartes' application of logic when seeking to understand the natural world produced many cutting edge contributions to philosophy, mathematics, and science. For example, it was Descartes who introduced skepticism as an essential part of the scientific method, which includes the contemporary practice of methodological skepticism. These contributions gave him great credibility. If Descartes said animals were stupid machines, then they must be.

Descartes' simple assurance of the superiority of humanity over animals even effectively silenced countless centuries of lessons, we had learned about animal behavior before his notorious birth in 1596. These lessons extended far back to our dim past as "Man the Hunter" whose survival depended on his knowledge of prey

behavior, but of the behavior of the predators that stalked him as well. These lessons are accumulated through the domestication of animals, discovery of agriculture, and establishment of farms and farm animals. They accrued through the age of grand estates – think cheetahs lounging in ancient Egyptian palaces – and more recently in animal collections on private estates and in zoological gardens, the latter in name only, because of the small, hard, empty cells we gave the animals to live in.

The point is that Descartes' simple proclamation that animals were stupid machines erected a wall that has been simultaneously invisible and omnipresent for the past three centuries. Those walls even surrounded universities, despite scholars' best efforts to study animal behavior objectively. Contemporary scholars of all forms of animal behavior have all been thoroughly basted and baked in the Cartesian animals-are-stupid-machines attitude, a reality that demands their most profound consideration.

In this author's own lifetime, a few intrepid individuals dared to scale those tall and terrible Cartesian walls. One was a boy born in 1948 in the land of tulips and windmills (Den Bosch, the Netherlands). His mother taught him that the saddest sight was a bird in a cage. This kind of thinking, along with exposure to the brilliant ethologists of his day, gave the boy his special sympathy for animals. He henceforth developed a single-minded desire to understand animals clearly and realistically on their own terms. Unbeknownst to the earnest lad who went on to study biology in Nijmegen and Groningen, the Netherlands, his single-minded desire meant spending his life slamming his shoulder against Descartes' invisible wall.

He did his PhD project at Utrecht University. As he patiently recorded aggressive behavior among macaques, he saw the glimmerings of the other side of aggression: peacemaking. To earn some money, the sprouting young man helped the psychologists in Nijmegen, the Netherlands, who worked with chimpanzees. When Frans de Waal saw the chimps, it was love at first sight.

It is hard to doubt someone you love. But Frans knew for himself what Descartes said famously

aloud, "If you would be a real seeker after truth, it is necessary that at least once in your life you doubt, as far as possible, all things." Frans has done exactly that – doubt – systematically and empirically across his entire career. Frans used Descartes' own methodological skepticism against his terribly unjust invisible walls by questioning the claim that animals were stupid machines.

So Frans studied chimpanzees with fresh eyes, questioning the answers. Could all this bowing, bravado, kissing, and alliance shifting really occur without the chimps grasping at least the basics of planning, social calculations, and consequences? Did conflict *really* disperse opponents? Frans' discovery of chimpanzee politics and peacemaking was his first big shoulder shove against that invisible Cartesian wall. The wall creaked.

And he gave the rest of us a foothold. He refined the technique of providing empirical evidence for reconciliation when he designed a user-friendly, empirically elegant method. This wedged open a sliver of a slit in that invisible Cartesian wall. It has since widened considerably with the passage of scores of investigators who used Frans' PCMC method to reveal peacemaking in other species, including my own demonstration of reconciliation in bottlenose dolphins.

The author met Frans when he came to study the bonobos at the San Diego Zoo, where she worked. He was just the "guy from Europe." He was fun. He did not fanfare the guts it took to put "chimpanzee" and "politics" together in the title of a book. Nor did he complain that the tenor of the times insisted that his use of the word reconciliation (to describe peacemaking gestures after two chimps fought) was inevitably attended by the caveat "heuristic label" because, after all, animals were not exactly robotic automatons, but almost.

Frans kept heaving his shoulder against that invisible Cartesian wall. He led contemporary students of animal behavior and cognition in another direction with cross-fostering experiments. These not only demonstrated that peacemaking has a strong learning component. They encouraged animal behaviorists to conduct observation-based experiments. No Skinner box is needed.

Frans heaved his mighty shoulder against that invisible Cartesian wall again when he demonstrated how mere observation could be used to reasonably correlate behaviors that were staggered in time: I groom you this morning. You share food with me this afternoon. Who thought animals were paying attention like that? The chimps taught Frans that social interaction was a transaction. No exchange was without impact. This time, a couple of big boulders tumbled out of those invisible Cartesian walls.

Frans kept heaving. In turning Cartesian skepticism around, Frans invoked possibilities of animal behavior that few others dared consider: planned social strategies that included third party interventions, cooperation, reciprocity, and peace-making, but also justice, altruism, fairness, consolation, food sharing, and generosity. With such a tool chest, social interaction becomes a series of transactions with consequences. Animals had to remember and to think ahead.

Citing parsimony, Frans argued for evolutionary continuity with empirical evidence that empathic and cooperative tendencies are continuous across species. He argued that empathy is one of the emotional roots of morality. It had evolutionary roots far deeper than our own. Equitable attitudes are universal mammalian characteristics. Though the idea remains unwelcome in many quarters, one conclusion had to be that nonhuman great apes and humans are simply different types of apes. Nonetheless, humans are more systematically brutal than chimps and more empathic than bonobos. "Our societies are never completely peaceful, never completely competitive, never ruled by sheer selfishness, and never perfectly moral," Frans pointed out when calling us the bipolar ape!

No one familiar with Frans' work has to be persuaded that he has unique vision. His penetrating views of the cognitive basis of animal behavior have given us a rich vocabulary for seeing animal behavior the way digital glasses give a 3D image in profound depth, color, and realism.

Little wonder that Frans is C. H. Candler Professor of Psychology at Emory University

and the Director of the Living Links Center at the Yerkes National Primate Research Center and has been a University of Utrecht Distinguished Professor since 2014. In 2007, Time magazine included him in the "TIME 100: The People Who Shape Our World," a list of the 100 most influential people. He was elected to the Dutch Academy of Sciences in 1993 and to the National Academy of Sciences in 2004. His books have been translated into over 20 different languages, and he probably wrote one in the time it took me to write this biography. He is married and lives close to Atlanta, where he and his wife Catherine throw generous parties so their graduate students can enjoy a moment of misty equality.

Frans told this author that he thought his greatest contribution to animal behavior and cognition studies was probably his discoveries of conflict resolution and empathy. To this author, Frans' greatest contribution was role modeling *how* to tease evidence out of benign observation by designing experiments that did not traumatize anybody involved – except Lance the capuchin, whose tantrum-like recognition of the unfairness of getting a cucumber reward when his compatriot got a grape went viral on the Internet!

Frans has worked single mindedly to put animals in a whole new light and reverse the appalling Cartesian sanction to brutalize them with impunity. Frans is not the only animal behaviorist to assault those invisible Cartesian walls with an academic battering ram, as this encyclopedia amply portrays. It was just that Frans' ram grew huge with time, and he hit those walls harder and more often than most. The last time this author saw Frans, she thanked him for casting such a bright light that so many of us could bask in his reflected glory. Frans' greatest contribution to animal cognition was to storm those Cartesian walls open. Because of his work, contemporary students of animal behavior and cognition are free today to actually explore these fascinating topics without the constraints of the past.

Frans, how does it feel to be your very own personal paradigm shift?

## Cross-References

- ▶ [Agonistic Behavior](#)
- ▶ [Ape Cognition](#)
- ▶ [Chimpanzees](#)
- ▶ [Conflict](#)
- ▶ [Great Ape Trust](#)
- ▶ [Primate Cognition](#)

## References

- Aureli, F., & de Waal, F. (Eds). (2000). *Natural conflict resolution*. Berkeley: University of California Press. ISBN 0-520-21671-7.
- de Waal, F. (1982). *Chimpanzee politics: Power and sex among Apes* (25th Anniversary ed.). New York: Harper and Row; 2007.
- de Waal, F. (1989). *Peacemaking among primates*. Cambridge, MA: Harvard University Press. isbn:0-674-65920-1.
- de Waal, F. (1996). *Good natured: The origins of right and wrong in humans and other animals*. Cambridge, MA: Harvard University Press. isbn:0-674-35660-8.
- de Waal, F. (2001a). *Tree of origin: What primate behavior can tell us about human social evolution*. Boston, MA: Harvard University Press. isbn:0-674-00460-4.
- de Waal, F. (2001b). *The Ape and the Sushi master; cultural reflections by a primatologist*. New York: Basic Books. isbn:0-465-04175-2.
- de Waal, F. (2005). *Our inner ape*. New York: Riverhead Books. isbn:1-57322-312-3.
- de Waal, F. (2006). *Primates and philosophers: How morality evolved*. Princeton, NJ: Princeton Science Library. isbn:0-691-12447-7.
- de Waal, F. (2009). *The age of empathy: Nature's lessons for a kinder society*. Toronto Ontario: McClelland & Stewart. isbn:978-0-307-40776-4 (reviewed in American Scientist).
- de Waal, F. (2016). *Are we smart enough to know how smart animals are?* New York, NY: Norton & Co. isbn:978-0-393-24618-6.
- de Waal, F., & Lanting, F. (1997). *Bonobo: The forgotten ape*. Berkeley: University of California Press. isbn:0-520-20535-9.
- de Waal, F., & Tyack, P.L. (eds) (2003). *Animal social complexity: Intelligence, culture, and individualized societies*. Cambridge, MA: Harvard University Press. isbn:0-674-00929-0.
- Weaver, A. (2003). Conflict and reconciliation in captive bottlenose dolphins, *Tursiops truncatus*. *Marine Mammal Science*, 19(4), 220–230.
- Weaver, A., & de Waal, F. (2002). An index for measuring relationship quality based on attachment theory. *Journal of Comparative Psychology*, 116, 93–106.
- Weaver, A., & de Waal, F. (2003). The mother-offspring relationship as template for social development: Reconciliation in Brown Capuchins (*Cebus apella*). *Journal of Comparative Psychology*, 117(1), 101–110.
- Wrangham, R.W., McGrew, W. C., de Waal, F.M., & Heltne, P. (Eds). (1994). *Chimpanzee cultures*. Foreword by Jane Goodall. Cambridge, MA: Harvard University Press. isbn:0-674-11662-3.

# C

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## Crocodylia Diet

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## Synonyms

[Behavior](#); [Foraging](#)

## Introduction

Crocodylians (crocodiles, caimans, alligators, gavials, and their kin) superficially resemble large lizards, but they are in fact more closely related to birds, with which they share many behavioral, and presumably cognitive, characteristics. Both belong to the Archosaur clade, which included dinosaurs and pterosaurs, as well as the ancestors of the present day crocodylians. The pterosaurs and most of the dinosaurs succumbed to a catastrophe, usually attributed to a meteorite impact at the Permian-Triassic boundary. However, one group of dinosaurs, the birds, survived and still dominates the landscape in most parts of the world. The ancestors of the crocodylians were diverse, often terrestrial predators, but all present-day members of this lineage are semiaquatic predators living at the interface between land and water.

The legacy of their terrestrial ancestors is revealed when crocodylians walk with their bodies held high off the ground with the legs propped almost vertically in contrast to the splayed-legged gait of lizards. Some crocodylians will even gallop if they need to return quickly to water, but the legs are generally used only to steer the body in shallow water. Most of a crocodylian's propulsive power comes from sweeps of its powerful tail through the water, and this restricts its foraging strategies and the vulnerability of different types of prey.

## Food and Feeding Habits

The metabolism of crocodylians is very slow, which has the advantage that they use energy very efficiently and do not have to feed frequently (Coulson and Hernandez 1983). Small- and medium-sized crocodylians can go for months without feeding, and the largest individuals can possibly survive fasts lasting several years. Many female crocodylians guard their nests during the two- to three-month incubation period, and if the nest is far from water she may not be able to feed. Female common caimans guarding nests far from water lose body condition during the incubation period in central Amazonia, but the time she can spend beside the nest may be more limited by water than energy.

The slow metabolism of crocodylians has allowed researchers to study digestive processes that

would be impossible to study in typical laboratory animals, such as rats, so our knowledge of the basic physiology of digestion owes much to the study of crocodilians. The slow metabolism is not a primitive feature, and presumably the terrestrial ancestors of present-day crocodilians had much higher metabolic rates and more active life styles. Rather, it is an adaptation that allows crocodilians to obtain much higher densities and biomass per unit area than similar-sized mammals (Magnusson and Lima 1991).

Their low metabolic rates allow crocodilians to spend long periods under water, either to escape from predators or to remain concealed from their terrestrial prey. Crocodilians sometimes forage underwater, and some species are known to take terrestrial prey well away from water, but most of their prey, including aquatic organisms, such as fish, is taken in the shallows or close to the bank, so that the head is out of the water at the moment the jaws are swept toward the prey. The basic tactic for prey capture is therefore a forward lunge propelled by the tail combined with a sideways sweep of the long jaws. There are only minor variations on this theme, so most of the cognitive input in feeding relates to where and when an attack should take place for a given prey type.

Because crocodilian metabolism is tuned to low energy expenditure, they are not well adapted to prolonged activity. Strenuous exercise leads to a buildup of lactic acid in their tissues, to which they are more tolerant than most vertebrates, but they still have to rest to repay the oxygen debt. Prolonged struggling during capture can even lead to the death of large individuals, which have more difficulty flushing their muscles with oxygenated blood than do small animals.

People who are considered intelligent are often described as “quick,” which implies that intelligence is associated with the ability to make quick decisions. However, a generally slow lifestyle and only small windows of time in which strenuous exercise is possible require complex planning and the ability to modify tactics during a feeding rally. Presumably, crocodilians need to keep complex maps in their heads in order to be in the right place at the right time to capture prey.

Some crocodilians, especially in the genus *Crocodylus*, undertake long annual migrations between feeding and breeding areas, some species make long marine voyages, and individuals have found their way back to their home ranges after being transported hundreds of kilometers along the coast to another river system. Young alligators have been shown to be able to use magnetic orientation to find their way home. Crocodilians therefore must have complex mental maps of the world, but it is unknown to what extent olfaction, visual landscape features, magnetic compass orientation, and celestial navigation play in crocodilian movement planning.

Crocodilians are often described as having a generalist diet, which could give the wrong impression about how they feed. It is true that crocodilians are able to take advantage of most types of animal prey that are of the right size, so analysis of stomach contents of a large number of individuals will reveal a wide range of prey types. However, this does not mean that individuals wander around opportunistically taking any animals that come too close. At any one time, an individual is likely to be specializing on a particular type of prey and modifying its behavior to maximize the probability of contact with food that gives the highest return in terms of energy or nutrients.

Several species of crocodiles have been seen using their bodies and tails to coral fish in shallow water. The crocodile lies with its body parallel to the bank and uses its tail to block movement of fish along the bank or to sweep them toward the snout. When the fish tries to escape past the crocodile's head, it is grabbed by a sideways sweep of the jaws. The crocodile does not even need to see the fish, because it has pressure-sensitive pits along its jaws which are thought to be able to detect water movements caused by swimming prey.

Caimans have been observed waiting under frogs that call from trees, but lay eggs in the stream. Presumably, the caiman has learned that calling frogs eventually descend to the edge of the stream, often leading a female into the jaws of the caiman as well. During floods, the same caimans position themselves perpendicular to the water



flow with the lower jaw just below water level and the upper jaw held just above it so that they can catch hapless animals being washed down. It is likely that both of these are learned behaviors.

One of the most spectacular sights on the East African savannas is the seasonal migration of wildebeest and other large ungulates. The herds cross the rivers at the same place each year and the crocodiles accumulate at these sites days or weeks before they arrive, indicating that crocodiles have very good long-term memories and can think ahead, as well as understanding spatial relationships.

Some caimans and crocodiles have been seen aggregated around canals where fish are funneled during migrations. Whether they find these aggregations alone, are only attracted by the concentration of other crocodylians, or are actively lead to feeding locations by other individuals is unknown. However, the latter is not unlikely. Caimans in the Brazilian Pantanal have been observed undertaking coordinated movements between pools in the dry season; one individual, usually the largest, leading the others, which follow in single file, sometimes for kilometers (Campos et al. 2003).

Because crocodylians often occur in large concentrations, social intelligence can be as important as hunting ability and not just because it is wise to follow the most experienced leader. Crocodylians have evolved into some of the most spectacular vertebrate killing machines that can bring down prey as large as themselves or, more importantly, kill another crocodylian with a single bite. Crocodylians do fight and kill each other, especially in territorial disputes. However, considering the high densities at which many species occur, fights are rare, and usually settled by one of the combatants showing submissive behavior, such as lifting its head vertically and revealing its throat.

Both crocodiles and caimans have been observed in narrow channels during fish migrations. Rather than attack haphazardly, the crocodylians form a line or a semicircle, all equally spaced, making a trap for the migrating fish. The predators do not break ranks even if the concentration of fish moves temporarily from one animal to another.

African crocodiles often have unexpected windfalls, such as a dead hippopotamus or elephant close to the water. Dozens or, in some cases, more than 100 crocodiles may gather at the carcass, but they can only feed from a small area of the soft underbelly, so the most efficient system is for them to take turns and that is exactly what they do, each individual waiting for their turn like gentlemen around a dinner table. Once an animal has pulled off a piece of meat, it moves out of the area to give the others access. There is obviously tension and all the crocodiles would probably like to be first to feed, but they apparently know their position in a hierarchy of dozens or more individuals, even though they only encounter each other sporadically in the river.

Most aquatic habitats show strong seasonal changes in water depth, inundation of marginal vegetation, and the types of prey animal found on the banks. It is therefore likely that individuals of all species of crocodylians adjust their foraging behavior in relation to seasonal structural changes in the habitat and concentrations of different prey, and that they learn to adapt their behavior in expectation of changes before they occur, as has been shown for African crocodiles. However, because most crocodylians forage mainly at night and are secretive, especially if they have been hunted, there are no direct observations to back up these speculations.

All crocodylians must change their foraging tactics throughout their lifetime simply because their size, and hence the type of prey they take, changes drastically over time. Juveniles of all species are small, about as big as a medium-sized lizard, and they increase more than a thousand times in weight before becoming sexually mature; individuals of some species being among the largest terrestrial predators on the planet.

Crocodylians have conical teeth that vary in size, but not much in shape. They are good for holding prey but are not adapted for cutting or grinding. Therefore, crocodylians usually swallow their prey whole or tear off large chunks that are thrown backward toward the throat and are swallowed principally due to gravity. To dismember its prey, a crocodylian has to take a firm hold and then spin its body to separate the piece held in

its mouth. This process depends on inertia and is more effective for large prey and large crocodilians. Dismemberment of prey is uncommon in small crocodilians.

The conical teeth are effective for holding prey but suffer severe stress during biting and when the crocodilian spins, and they are frequently broken or pulled out. Fortunately for the predator, crocodilian teeth that are lost during feeding are soon replaced by another that grows up from the same tooth socket.

Crocodylians have the strongest stomach acids of any group of vertebrates, so they can digest most animal matter, including bones. Nevertheless, assimilation efficiency is probably greater for food types similar to that of the bodies of crocodilians, such as vertebrate muscle, than for other material, such as invertebrate chitin. Most invertebrates are also small, so that it may not be worthwhile for larger crocodilians to hunt them. The ontogenetic shift in diet is probably the most studied aspect of food habits in crocodilians and the pattern is similar in almost all species.

African crocodiles (*Crocodylus niloticus*) up to about half a meter long eat mainly insects and spiders. Individuals between 2 and 4 m eat mainly fish and snails, and animals over 4 m eat mainly mammals, but also some reptiles and fish (Cott 1961). A similar pattern is seen in all species of crocodilians, but some change the types of prey at smaller sizes, and some never make the transition to eating mainly mammals.

There are probably several reasons that small crocodilians eat mainly insects and spiders. The first is that these are probably the most common prey within the size range that they can swallow. However, capturing terrestrial vertebrates probably requires stealth and understanding of the surrounding habitat. Recently hatched crocodilians usually form crèches that are accompanied by their mother for the first few weeks or up to 2 years in some cases. Soon after, the juveniles start to disperse, probably egged on in their movements by territorial adults for the decade or more they take to get to breeding size. During that time, they may not remain in any one area long enough to develop a useful hunting map.

Large juveniles and sub adults usually eat mainly crustaceans, mollusks, and fish, the proportions depending on availability within the habitats the species occupies. Although even large crocodilians will occasionally take insects or other invertebrates, the energetic contribution of these groups tends to be negligible, and it is unlikely that large crocodilians actively seek these prey types unless they occur in unusually large concentrations.

The largest crocodilians often eat a large proportion of mammals, and these probably represent the most digestible food packets available. However, they are also often hard to catch and come close to water infrequently. Therefore, the strategies that crocodilians use to catch them are likely to be different from those used to catch widely distributed prey, such as insects, or prey that occurs in predictable places, such as fish.

Differences among size classes in the type of prey eaten depend to a certain extent on the seasonal differences in habitats. In places with large inundated floodplains, such as flooded savannas and forests, and hence large seasonal differences in access to different habitats, diets tend to differ less between size classes, because all must move with the advancing flood waters. In habitats with less seasonal variation, such as rivers and lakes, different size classes tend to segregate in different habitats and differences are more pronounced.

The species with the greatest divergence from the usual size-related changes in diet is Schneider's dwarf caiman, *Paleosuchus trigonatus*. It lives in dense Amazonian rainforest with little primary productivity in the understory. Therefore, insects and mollusks tend to be less abundant and individuals less than a meter long eat many frogs, snakes, and other small vertebrates. Fish, which tend to be scarce in the small streams are never found in abundance in its diet and the diminutive adults, which rarely reach two meters long, eat many mammals, including pacas, porcupines, and monkeys. As porcupines and monkeys rarely descend to the edge of the stream, it is hard to imagine what strategy this species uses to capture them. They must be very successful, as they maintain higher biomass than all the mammalian carnivores together in the same type of habitat.

It is often claimed that snout-shape in crocodilians reflects their diet, fish-eating species having long, thin snouts, and species that take large prey, such as ungulates, having heavier, wider snouts. However, this is only partially true. Species that live in open-water habitats tend to have thinner snouts, but they are not any longer in relation to body length. It makes sense to have a thin snout, which causes less resistance, if you live in open water, whether you eat fish or not. Fish just happen to be the nutritionally most valuable prey in open-water habitats.

The species of crocodilians that eat the most large ungulates and other large mammals, the estuarine crocodile, *Crocodylus porosus*, and the Nile crocodile, have snouts of intermediate width, which can be considered a generalized form for crocodilians. This form of snout appears to be adequate to withstand the stresses of capturing large prey in relation to the size of the crocodilian.

The species of crocodilians with the widest snouts, including extinct forms, do not feed on the largest prey, but all live or lived in densely vegetated habitats, such as marshes, so it seems that extreme widening of the snout is an adaptation to smashing through thick vegetation rather than protection against breakage while pulling down large prey.

## Conclusion

In summary, we know quite a bit about the morphological and physiological adaptations of

crocodilians associated with feeding and digestion, but because of their nocturnal cryptic habits we know little about the cognitive and behavioral adaptations that have led them to be the most successful and persistent nonflying Archosaurs.

## Cross-References

- ▶ [Crocodylia Cognition](#)
- ▶ [Crocodylia Communication](#)
- ▶ [Crocodylia Life History](#)
- ▶ [Crocodylia Locomotion](#)
- ▶ [Crocodylia Morphology](#)
- ▶ [Crocodylia Navigation](#)
- ▶ [Crocodylia Sensory Systems](#)

## References

- Campos, Z., Coutinho, M., & Magnusson, W. E. (2003). Terrestrial activity of caiman in the Pantanal, Brazil. *Copeia*, 2003, 628–634.
- Cott, H. B. (1961). Scientific results of an inquiry into the ecology and economic status of the Nile Crocodile (*Crocodylus niloticus*) in Uganda and Northern Rhodesia. *Journal of Zoology*, 29, 211–356.
- Coulson, R. A., & Hernandez, T. (1983). Alligator metabolism. Studies on chemical reactions in vivo. *Comparative Biochemistry and Physiology B*, 74, 1–182.
- Magnusson, W. E., & Lima, A. P. (1991). The ecology of a cryptic predator, *Paleosuchus trigonatus*, in a tropical rainforest. *Journal of Herpetology*, 25, 41–48.

# G

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## Gordon Gallup

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### Mirror Self-Recognition

In 1969, he conducted an experiment designed to determine if chimpanzees could recognize themselves in mirrors (Gallup 1970). Although chimpanzees initially respond to mirrors as though they were seeing other chimpanzees, after a couple of days the chimpanzees began to use the reflection to respond to themselves. As an objective test of self-recognition he developed the mark test, where anesthetized chimpanzees were marked with a red, odorless, nonirritating dye on the top half of an eyebrow ridge and the upper half of the opposite ear. Upon recovery from anesthesia, he discovered that the chimpanzees used the mirror to touch and investigate the red marks on their faces that could only be seen in the mirror.

These findings have been widely replicated with chimpanzees and extended to include orangutans and humans. Early attempts to adapt this methodology for use with children, however, were seriously flawed (Gallup 1994). The capacity for mirror self-recognition in other species is widely debated, but as yet the evidence is not conclusive (Anderson and Gallup 2015).

The mark test has been cited as the “gold standard” for assessing self-recognition, and it has survived multiple challenges, including the idea that it may be an artifact of species differences in face touching behavior (Suarez and Gallup 1986) or an artifact of anesthetization (Povinelli et al. 1997), along with claims that failures to find self-recognition may be due to gaze aversion (Anderson and Roeder 1989), a lack of interest in superimposed body marks (Gallup et al. 1980), or that the presence of a human researcher may inhibit or distract subjects from investigating the marks (Shillito et al. 1999). Pervasive species differences in mirror self-recognition continue to prevail in spite of attempts to argue for the possibility of self-recognition in other modalities (Platek et al. 2004), along with repeated but unconvincing attempts to engineer self-recognition in other species (Anderson and Gallup 2015) and unsupported claims that self-recognition has nothing to do with self-awareness (Gallup et al. 2014).

More recently, Platek and Gallup developed a method for assessing self-recognition that involves showing people faces on a computer monitor, and they are instructed to press particular keys on the keyboard to indicate if it is a stranger’s face, a familiar face, or their own face (Platek et al. 2004). Rather than an all or none (pass/fail) approach to self-recognition, this paradigm can be used to quantify individual differences in self-face identification latencies measured in milliseconds and that has led to some striking results

implicating important and clinically relevant self-processing deficits (Platak et al. 2003).

Gallup's idea that self-awareness may be a springboard to being able to use your experience to model the experiences of others and make inferences about their mental states has also been controversial (Gallup 1982). The jury is still out about mental state attribution in chimpanzees and orangutans (Shillito et al. 2005), but for humans there are no documented instances of being able to take into account what others know, want, or intend to do without being able to recognize yourself. Likewise, deficits and developmental delays in self-recognition (e.g., autism) covary with mental state attribution deficits, and this also holds true for brain-damaged patients who are deficient in self-recognition as well as those who lose the capacity to recognize themselves due to mental illness (Gallup et al. 2003).

### **Tonic Immobility and Open Field Behavior**

Tonic immobility is triggered by the application of manual restraint, such as holding an animal down on a flat surface. Initially the animal will struggle and try to escape, but if you persist in holding the animal in place for several seconds it will go into a seemingly catatonic-like state of physical immobility which can last from a few minutes to over an hour or more after you remove your hands.

In a series of studies featuring many different species, Gallup and his students showed that laboratory procedures designed to increase fear (e.g., loud noise, conditioned aversive stimuli) prolong the response, while those that alleviate fear (e.g., handling, taming, tranquilizers) antagonize the reaction. Under natural conditions, the evidence shows that tonic immobility is one of several defensive reactions in a distance-dependent series of antipredator strategies (Gallup 1977). Tonic immobility depends on the integrity of neurological structures at the level of the brainstem, is associated with widespread autonomic involvement, and the duration of the response is related to changes in brain serotonin (Wallnau and Gallup 1977).

Examples of extreme behavioral inhibition in humans prompted Suarez and Gallup (1979) to theorize that "rape-induced paralysis" may be an instance of tonic immobility. As a result, the idea that certain states of behavioral inhibition in humans (e.g., rape, PTSD, catatonic schizophrenia) represent instances of tonic immobility has been embraced by a growing number of clinical psychologists (Marx et al. 2008). Tonic immobility is a useful means of modeling states of extreme behavioral inhibition under controlled laboratory conditions and may have important practical implications for how such states are dealt with in applied settings (Gallup and Rager 1996).

As an extension of this predator-prey model, Gallup undertook a series of studies to re-examine open field behavior. The point of departure for these studies was that what animals do when tested in an open field is a byproduct of predatory overtones associated with being contacted, handled, and tested by a human experimenter and also being socially separated from companions. This creates a classic approach/avoidance conflict, and predictions derived from this model are surprisingly accurate across a number of mammalian and avian species.

For example, the mere presence of someone in the room when animals are tested makes animals freeze longer. The further away the experimenter is from the open field and if the subjects cannot see his/her face the amount of time spent freezing diminishes. Likewise, animals that are placed by hand into the open field freeze longer than those that are mechanically introduced into the open field. According to this model, the initiation of movement in the open field represents an attempt to reinstate contact with companions. Consistent with this analysis, animals that are tested in pairs wait longer to begin moving and show fewer attempts to escape from the open field. In contrast, animals maintained in social isolation before testing wait longer to move (Gallup and Suarez 1980; Suarez and Gallup 1981, 1982).

Results such as these raise serious questions about the validity of open field testing as it has been traditionally used as a measure of emotionality.

## Human Reproductive Competition

In the 1980s, Gallup's attention began to focus on human behavior from an evolutionary perspective. Rather than being a matter of competition for scarce resources and the survival of the fittest, evolution is a matter of competition for gaining genetic representation in subsequent generations.

Work that Gallup and others have done that was inspired by this perspective has shown that the mere sound of a person's voice contains information about their sex, age, health, fertility, body configuration, facial attractiveness, grip strength, when they lost their virginity, how many sex partners they have had, their propensity for infidelity, and where they are in their menstrual cycle (for a review see Gallup and Frederick 2010).

Work from his lab has also shown that most people have found themselves attracted to someone only to discover that, after they kiss that person, they are no longer interested (Hughes et al. 2007). Thus, there may be hard-wired mechanisms activated at the moment of the first kiss that function to make a determination about whether this would be a good genetic/reproductive match. Sex is also a component to courtship, and sampling semen from different suitors may be analogous to kissing; i.e., either you wake up the next day head over heels in love or with feelings of regret for what you did the night before (Gallup and Reynolds 2014).

Most women have a guarantee of sharing half of their genes in common with their children. But, because of female infidelity, men have to contend with paternal uncertainty and the prospect of being cuckolded. Gallup's work on paternal assurance tactics has shown that men invest in children in relation to the presence of shared physical and psychological features (Gallup et al. 2016). Competition for paternity has even affected human genital morphology. Using laboratory simulations Gallup and his students have shown that the peculiar shape of the human penis evolved to compete with the presence of rival male semen in the woman's reproductive tract by promoting semen displacement and increasing the likelihood of paternity by the resident male (Gallup et al. 2003). This research prompted Satoshi Kanazawa

to conclude that "if you want to know what women have been up to, look at the human penis." The work on human genital morphology also led Gallup to raise the question among uncircumcised men of unwittingly piggybacking rival male semen captured under the foreskin from one vagina to the next (Gallup and Burch 2004), which inspired a recent novel "The Hitchhiker's Child" (Baker 2013).

As evidence for the impact of some of this work, it is worth noting that in 2017 the journal *Evolutionary Behavioral Sciences* published by the American Psychological Association listed seven of his former students as members of the editorial board (Rebecca Burch, Michael Frederick, Andrew Gallup, Marissa Harrison, Susan Hughes, Nathan Pipitone, and Steven Platek).

Some of Gallup's more controversial work on reproductive competition involves applying evolutionary theory to homosexuality (Gallup and Suarez 1982) and attitudes toward homosexuals (Gallup 1995). According to him, homosexuality is a byproduct of evolved differences between men and women in fitness maximization strategies and as a consequence everyone has the capacity to become homosexual. Likewise, his view of homophobia as a byproduct of natural selection implies that everyone (including homosexuals) will exhibit homophobia under certain conditions.

## Yawning as a Brain Cooling Mechanism

While most of Gallup's research continues to focus on human reproductive competition about 10 years ago he became interested in yawning, which is something we all do but was not well understood. In contemplating what happens during the execution of a yawn, it occurred to him that yawning might function as an evolved brain cooling mechanism.

Just as is true for metabolism elsewhere in the body, brain metabolism generates heat and research had shown that one of the rate-limiting steps to how big brains can get is dependent upon the development of mechanisms that function to dissipate heat and cool the brain (Falk 1990). As evidence for the idea that yawning may be one of



several mechanisms that function to maintain thermal homeostasis in the central nervous system, Gallup and his son Andrew found that nasal breathing and forehead cooling antagonizes yawning in college students (Gallup and Gallup 2007). They also found that rats with temperature probes implanted in the frontal cortex exhibited consistent increases in brain temperature prior to yawning, with brain temperature returning to baseline within seconds after the execution of a yawn (Shoup et al. 2010). Additional work has confirmed the existence of a thermal window that constrains yawning at ambient temperatures that rise to body temperature or approach freezing (Gallup and Eldakar 2013). A recent comparative study inspired by Andrew Gallup found positive correlations that exceeded .9 between species differences in yawn duration and both brain weight and number of cortical neurons (Gallup et al. 2016). As brains get bigger yawns last longer.

Numerous medical problems are related to thermoregulation (e.g., multiple sclerosis) and emerging evidence suggests that excessive yawning in humans may be a diagnostic red flag for central nervous system thermoregulatory dysfunction (Gallup and Gallup 2008).

Contrary to popular opinion, yawning is a compliment. Because yawns appear to function to cool metabolically overheated brains, if someone yawns the next time you are talking with them do not take it as an insult. Rather than a sign of boredom, yawning is an indication that mechanisms have been activated to maintain attention and promote optimal cognitive processing.

Other aspects of Gallup's research are also related to thermoregulation. His work with Jessica Ash on the impact of climate change on brain evolution suggests that global warming may be undermining the conditions that gave rise to big human brains during the last ice age (Ash and Gallup 2007). And because the scrotum functions to cool the testicles, he has theorized that descended testicles evolved to capitalize on the conditional increase to body temperature that occurs when sperm are released into the vagina which functions to induce a time-bound activation of sperm (Gallup et al. 2009).

It should be clear from this brief overview that rather than being focused and pedantic, Gallup's interests have been very broad and driven by theory construction and hypothesis testing. One of his least cited but most interesting papers involves our reliance on visual metaphors to capture different mental states, which may be a byproduct of our earlier adaptation to life in the trees as arboreal primates (Gallup and Cameron 1992).

## Cross-References

- ▶ [Concealed Ovulation](#)
- ▶ [Frequency of Sex](#)
- ▶ [Orgasm](#)
- ▶ [Reproductive Rate](#)
- ▶ [r vs. K Selection](#)
- ▶ [Semen Familiarity](#)

## References

- Anderson, J. R., & Gallup Jr., G. G. (2015). Mirror self-recognition: A review and critique of attempts to promote and engineer self-recognition in primates. *Primates*, 56, 317–326.
- Ash, J., & Gallup Jr., G. G. (2007). Paleoclimatic variation and brain expansion during human evolution. *Human Nature*, 18, 109–124.
- Baker, R. (2013). *The hitchhiker's child*. HARD NUT books.
- Falk, D. (1990). Brain evolution in Homo: The “radiator” theory. *Behavioral and Brain Sciences*, 13(2), 333–344. (1990).
- Gallup Jr., G. G. (1970). Chimpanzees: Self-recognition. *Science*, 167, 86–87.
- Gallup Jr., G. G. (1977). Tonic immobility: The role of fear and predation. *Psychological Record*, 27, 41–61.
- Gallup Jr., G. G. (1982). Self-awareness and the emergence of mind in primates. *American Journal of Primatology*, 2, 237–248.
- Gallup Jr., G. G. (1994). Self-recognition: Research strategies and experimental design. In S. Parker, R. Mitchell, & M. Boccia (Eds.), *Self-awareness in animals and humans* (pp. 35–50). Cambridge, GBR: Cambridge University Press.
- Gallup Jr., G. G. (1995). Have attitudes toward homosexuals been shaped by natural selection? *Ethology and Sociobiology*, 16, 53–70.
- Gallup Jr., G. G., & Cameron, P. A. (1992). Modality specific metaphors: Is our mental machinery “colored” by a visual bias? *Metaphor and Symbolic Activity*, 7, 93–98.

- Gallup, A. C., & Eldakar, O. T. (2013). The thermoregulatory theory of yawning: What we know from 5 years of research. *Frontiers in Neuroscience*, *6*, 188. doi:10.3389/fnins.2012.0018.
- Gallup Jr., G. G., & Frederick, D. A. (2010). The science of sex appeal: An evolutionary perspective. *Review of General Psychology*, *14*, 240–250.
- Gallup, A. C., & Gallup Jr., G. G. (2007). Yawning as a brain cooling mechanism: Nasal breathing and forehead cooling diminish the incidence of contagious yawning. *Evolutionary Psychology*, *5*, 92–101.
- Gallup, G. G., & Burch, R. L. (2004). Semen displacement as a sperm competition strategy in humans. *Evolutionary Psychology*, *2*, 12–23.
- Gallup, A. C., & Gallup Jr., G. G. (2008). Yawning and thermoregulation. *Physiology and Behavior*, *95*, 10–16.
- Gallup Jr., G. G., & Rager, D. R. (1996). Tonic immobility as a model of extreme states of behavioral inhibition: Issues of methodology and measurement. In P. R. Sanberg, K.-P. Ossenkopp, & M. Kavaliers (Eds.), *Motor activity and movement disorders* (pp. 57–80). Totowa: Humana Press.
- Gallup Jr., G. G., & Reynolds, C. J. (2014). Evolutionary medicine: Semen sampling and seminal plasma hypersensitivity. *Evolutionary Psychology*, *12*, 245–250.
- Gallup Jr., G. G., & Suarez, S. D. (1980). An ethological analysis of open-field behaviour in chickens. *Animal Behaviour*, *28*, 368–378.
- Gallup Jr., G. G., & Suarez, S. D. (1982). Homosexuality as a byproduct of selection for optimal heterosexual strategies. *Perspectives in Biology and Medicine*, *26*, 315–322.
- Gallup Jr., G. G., Wallnau, L. B., & Suarez, S. D. (1980). Failure to find self-recognition in mother-infant and infant-infant rhesus monkey pairs. *Folia Primatologica*, *33*, 210–219.
- Gallup Jr., G. G., Anderson, J. R., & Platek, S. M. (2003). Self-awareness, social intelligence, and schizophrenia. In T. Kircher & A. S. David (Eds.), *The self in neuroscience and psychiatry* (pp. 147–165). Cambridge, UK: Cambridge University Press.
- Gallup Jr., G. G., Burch, R. L., Zappieri, M. L., Parvez, R. A., Stockwell, M. L., & Davis, J. A. (2003). The human penis as a semen displacement device. *Evolution and Human Behavior*, *24*, 277–289.
- Gallup Jr., G. G., Finn, M. M., & Sammis, B. (2009). On the origin of descended scrotal testicles: The activation hypothesis. *Evolutionary Psychology*, *7*, 517–524.
- Gallup Jr., G. G., Platek, S. M., & Spaulding, K. N. (2014). The nature of visual self-recognition revisited. *Trends in Cognitive Science*, *18*, 57–58.
- Gallup, A. C., Church, A. M., & Pelligrino, A. J. (2016). Yawn duration predicts brain weight and cortical neuron number in mammals. *Biology Letters*, *12*, 20160545. doi:10.1098/rsd.2016.0545.
- Gallup Jr., G. G., Ampel, B. C., Matteo, D. Y., & O'Malley, E. E. (2016). Behavioral resemblance and paternal investment: Which features of the chip off the old block count? *Evolutionary Behavioral Sciences*, *10*, 1–9.
- Hughes, S. M., Harrison, M. A., & Gallup Jr., G. G. (2007). Sex differences in romantic kissing among college students: An evolutionary perspective. *Evolutionary Psychology*, *5*, 612–631.
- James R. Anderson, Jean-Jacques Roeder. (1989). Responses of capuchin monkeys (*Cebus apella*) to different conditions of mirror-image stimulation. *Primates*, *30*(4):581–587.
- Marx, B., Forsyth, J., Gallup Jr., G. G., Heidt, J. M., & Fuse, T. (2008). Tonic immobility as an evolved predator defense: Implications for sexual assault survivors. *Clinical Psychology: Science and Practice*, *15*, 74–90.
- Platek, S. M., Myers, T. E., Critton, S. R., & Gallup Jr., G. G. (2003). Left-hand advantage for self-description: The impact of schizotypal personality traits. *Schizophrenia Research*, *65*, 147–151.
- Platek, S. M., Thompson, J. W., & Gallup Jr., G. G. (2004). Cross-modal self-recognition: The role of visual, auditory, and olfactory primes. *Consciousness and Cognition*, *13*, 197–210.
- Povinelli, D. J., Gallup Jr., G. G., Eddy, T. J., Bierschwale, D. T., Engstrom, M. C., Perilloux, H. K., & Toxopeus, I. B. (1997). Chimpanzees recognize themselves in mirrors. *Animal Behaviour*, *53*, 1083–1088.
- Shillito, D. J., Gallup Jr., G. G., & Beck, B. (1999). Factors affecting mirror behavior in western lowland gorillas, *Gorilla gorilla*. *Animal Behaviour*, *57*, 999–1004.
- Shillito, D. J., Shumaker, R. W., Gallup Jr., G. G., & Beck, B. B. (2005). Understanding visual barriers: Evidence for level 1 perspective-taking in an orangutan (*Pongo pygmaeus*). *Animal Behaviour*, *69*, 679–687.
- Shoup, M. L., Gallup, A. C., Gallup Jr., G. G., & McNay, E. C. (2010). Yawning and stretching predict brain temperature changes in rats: Support for the thermoregulatory hypothesis. *Frontiers in Evolutionary Neuroscience*, *2*, 1–5.
- Suarez, S. D., & Gallup Jr., G. G. (1979). Tonic immobility as a response to rape in humans: A theoretical note. *Psychological Record*, *29*, 315–320.
- Suarez, S. D., & Gallup Jr., G. G. (1981). An ethological analysis of open-field behavior in rats and mice. *Learning and Motivation*, *12*, 342–363.
- Suarez, S. D., & Gallup Jr., G. G. (1982). Open-field behavior in chickens: The experimenter is a predator. *Journal of Comparative and Physiological Psychology*, *96*, 432–439.
- Suarez, S. D., & Gallup Jr., G. G. (1986). Face touching in primates: A closer look. *Neuropsychologia*, *24*, 597–600.
- Wallnau, L. B., & Gallup Jr., G. G. (1977). A serotonergic, midbrain raphe model of tonic immobility. *Biobehavioral Reviews*, *1*, 35–43.

**Gordon G. Gallup, Jr** was born in 1941 and held his first faculty appointment in 1967 as an Instructor at Washington State University, where he got his Ph.D. in 1968. In the fall of that year, he accepted a position at Tulane University where he was promoted from Assistant to Associate

Professor in 1972 and to Full Professor in 1974. In 1975, he took a position at the State University of New York at Albany as Chair of the Psychology Department and served in that capacity for three consecutive 3-year terms. He continues to hold a position there as a faculty member. He served as the Editor of the **Journal of Comparative Psychology** from 1989 to 1994.

Most of Gallup's research has focused on the impact of evolution on behavior. Some aspects of his research are represented by work on the following four broad but not mutually exclusive categories.

# P

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## Personality in Animals

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### Synonyms

[Behavioral syndromes](#); [Individual differences](#);  
[Temperament](#)

### Introduction

What is personality? If asked this question, most people would have an intuitive sense of what the word “personality” means. When describing their pets, or animals at zoos, it would not be uncommon for someone to use terms such as curious, excited, or shy. However, pinning down a clear definition of personality is more challenging. In humans, personality refers to individual differences in patterns of thinking, feeling, and behaving (Gosling 2001). These patterns are thought to be stable across time, meaning that a person who tends to be excitable at one time point will also tend to be excitable a month later, although there are known changes that occur across a person’s life span (Roberts et al. 2006). Individual patterns are also thought to be stable across contexts. For example, someone who is curious about new people will also be curious about new aspects of their

environment. It is unfortunately not possible to ask an animal how they are thinking or feeling. As a result, the most commonly used definition of animal personality is individual differences in behavior that are consistent across time and contexts (Gosling 2001). Despite this, researchers have often shied away from labeling individual differences in behavior as “personality,” for fear of anthropomorphism (Gosling and John 1999). Instead, labels such as behavioral syndromes and temperament have been used interchangeably with personality. However, there must be measures that do not rely on verbal reports of thoughts or feelings, as personality has been repeatedly assessed in young children who are yet to develop language abilities (e.g., Thomas and Chess 1977). So, if we cannot ask an animal, or child, about their personality, what methods can we use?

### Measuring Animal Personality

The methods used to study animal personality can be categorized using two main criteria: the way in which measures are selected or the data collection method. Using the former criterion, methods can be distinguished as either predominantly top-down or bottom-up. Bottom-up procedures involve selecting measures that are specific to the studied species, therefore maximizing the likelihood of including relevant traits (Weiss and Adams 2013). However, this does mean that cross-species comparisons are made more

challenging, due to the variation in measures used in different studies. In contrast, top-down approaches adapt an existing model to create a measure for assessing another species (Freeman et al. 2011). This does run the risk of including traits that are irrelevant outside of the original model, but facilitates cross-species comparisons.

When using a top-down approach, a commonly adapted framework is the Five Factor Model (Goldberg 1990). This is a widely accepted model for human personality, and as the name suggests, it consists of five factors: Openness to Experience, Conscientiousness, Extraversion, Agreeableness, and Neuroticism. In this model, an individual with a high score on Openness to Experience tends toward traits such as imagination, creativity, and curiosity, while individuals who are self-disciplined and dutiful score highly on the Conscientiousness factor. The Extraversion factor describes an individual's tendency to be sociable, assertive, and active. Agreeableness contains traits such as trust, cooperation, and a lack of aggression, and finally, vulnerability to stress, anxiety, and depression describe the high pole of the Neuroticism factor.

The animal personality literature suggests that factors analogous to all of the human five factors are found in other species (Gosling and John 1999). In the most recent comprehensive review to date, a factor similar to Extraversion was found most frequently, in 90% of studies, across taxa as diverse as chimpanzees and octopuses. Analogues to Neuroticism and Agreeableness were almost as common, with all three of these factors emerging in cats, dogs, rhesus monkeys, gorillas, and chimpanzees. Openness-like dimensions were present in 7 of 12 species, which was at least partially attributed to methodological issues. Finally, although both cats and dogs possessed a factor combining Conscientiousness and Openness, only chimpanzees exhibited a pure Conscientiousness factor. Overall, this suggests that shared, general mechanisms may be responsible for the personality dimensions of Extraversion, Neuroticism, Agreeableness, and potentially Openness, although the specific behavioral manifestations of each differ between species. In contrast, Conscientiousness may be relatively young in

evolutionary terms, shared only by humans and our closest phylogenetic relatives.

Although there appears to be a considerable number of personality traits shared across species, there are clear species-specific differences in how these are manifested in behavior. For example, a cuttlefish classed as bold, similar to one facet of human Extraversion, spends more time at the top of the tank and produces a visual threat display in response to a predator (Carere et al. 2015). In contrast, an extraverted bottlenose dolphin may vocalize often and engage in a variety of play behaviors (Highfill and Kuczaj 2007). It is therefore important for specific features of any species to be carefully considered when assessing their personality. For instance, to assess aggressiveness as a personality trait in dolphins, it would be inappropriate to include the skin color threat displays seen in cuttlefish (Carere et al. 2015), but relevant to measure biting or ramming (Connor et al. 2000).

Instead of top-down versus bottom-up categorization, animal personality methods can be distinguished based on the method of data collection, of which there are two main types: behavioral coding and trait rating. Behavioral coding involves making observations of animals and recording the occurrence of behaviors of interest. Where naturalistic coding is used, animals are observed without any human intervention or manipulation, which can be in a captive or wild setting (Freeman et al. 2011). For example, the behavior of harbor seals and California sea lions has been recorded without experimenter interference (de Vere 2017). Using the frequencies of these behaviors, both species demonstrated two personality factors: boldness and routine activity. Bold seals and sea lions were active, alert, and more likely to move around on land, while highly routine individuals tended to swim in predictable patterns and rest little. In contrast, experimental coding involves making observations during behavioral tests. For example, hermit crabs have been assessed for personality using two tests: predator and open field (Watanabe et al. 2012). The responses of individual crabs were described using two behavioral dimensions. The first, named shy-bold, consisted of the time taken for

crabs to emerge versus hide in response to a predator. The second dimension was named exploration-avoidance, as it contained the measurements of exploration in a novel environment, the open field, and the time taken to emerge after the predator was removed.

The main alternative, trait rating, involves people judging individual animals on their tendencies on a number of trait words, such as curious or active. These judgments may be based on a rater's cumulative experience with the focal animal, as in the case of pet owners or zoo keepers (Freeman et al. 2011). An example of this can be seen in a personality assessment of bottlenose dolphins (Highfill and Kuczaj 2007). The dolphin population was housed at a facility where trainers were responsible for their daily care. These people rated the dolphins on traits such as reliable, curious, and playful, revealing individual scores that paralleled those found in humans (Goldberg 1990). Alternatively, judges may rate animals after having made a certain set of observations. For example, this design has been applied by having judges rate individual horses on traits such as exploration, vigilant, and submissive, after observing 2 hours of their behavior (Lloyd et al. 2007). This revealed six factors that explained the variation in ratings between horses, one of which was named sociability, as it consisted of traits such as sociable, playful, and popular.

## Why Do We Care About Animal Personality?

### Welfare

Now that we know that animals have personality, you may be wondering: why do we care? Well, personality has been linked to several interesting areas of research. One of the most important of these for the animals themselves is welfare. Commonly used indicators of poor animal welfare are stereotypic behaviors, which are defined as those that are repetitive, unvarying, and functionless (Mason and Latham 2004). Given that these behaviors are estimated to be exhibited by more than 85 million animals globally (Mason and Latham 2004), it is important to understand the

contributing factors, and growing evidence suggests that one of these is personality.

In one example of this, an interaction was found between rearing conditions and personality. Highly gentle or nervous 4-month-old rhesus macaques who were reared in indoor cages were more likely to exhibit stereotypic behaviors later in life (Vandeleest et al. 2011). The same effect was not seen for nervous or gentle macaques reared outdoors, therefore underscoring the subtle influence that personality can have on welfare outcomes. In another taxon, personality has also been found to mediate the effects of changes in environmental conditions. Parrots rated as highly extraverted developed fewer stereotypic behaviors while living in a barren environment (Cussen 2013). Low extraversion birds also maintained a higher level of stereotypies even after being reintroduced to a more complex, enriching environment.

However, there are issues associated with using stereotypic behaviors as indicators of poor welfare. One of these is that not all personality types seem to react in the same way to negative environments. A personality dimension along which animals can be characterized is the proactive-reactive axis. Proactive animals respond to stressful stimuli in an active manner, such as by exhibiting stereotypic behaviors. In contrast, those with reactive personalities are more likely to show passive responses, resulting in fewer stereotypic behaviors, despite exhibiting more drastic physiological markers of stress (Ijichi et al. 2013). Therefore, of two animals not exhibiting stereotypic behaviors, one with a reactive personality is more cause for concern than one with a proactive personality. Consequently, knowledge of animal personalities could allow welfare measures to be individualized for maximal well-being.

Personality is also associated with the extent to which animals interact with environmental enrichment. Although definitions of enrichment have changed over the years, a broad definition is increasing the choices available to animals and encouraging species-typical behavior by providing physical, mental, and social stimulation (Kulpa-Eddy et al. 2005). Improving animal welfare is frequently cited as the primary function of



providing environmental enrichment, but the needs and preferences of individual animals are often not taken into account.

Most of the evidence suggesting that personality mediates the effectiveness of various types of enrichment comes from studies of chimpanzees, involving research or training participation. In one such study, cognitive tasks involving selecting answers on a screen were thought to be potentially enriching. However, even when these tasks were familiar, chimpanzees characterized as stress sensitive exhibited increased self-directed behaviors, such as scratching, after providing an incorrect answer (Yamanashi and Matsuzawa 2010). High scores on the Openness personality dimension have also been associated with voluntary participation in potentially enriching interactions with humans. For example, high-Openness chimpanzees chose to spend more time engaged in research activities (Herrelko et al. 2012), as well as successfully completing a voluntary medical sampling procedure in the first session (Reamer et al. 2014).

In a study of a different species, snow leopards, novel objects were provided as a form of environmental enrichment. Leopards who visited these objects more also scored highly on one or both of the personality dimensions of Active/Vigilant and Curious/Playful (Gartner and Powell 2012). This provides two potential implications for using novel objects as enrichment for these animals. Firstly, novel objects may not be effective for providing enrichment for leopards with low scores on Active/Vigilant and Curious/Playful. Secondly, individuals with high scores on these dimensions may visit the objects more and therefore derive greater enrichment value from them. However, they may also become bored faster and require more frequent changes in enrichment provisioning to maintain potential welfare benefits.

Finally, several authors have made suggestions for individualized housing provisions, based on personality assessments. For example, cheetahs with high scores on the tense-fearful dimension were rated as being fearful, insecure, and tense (Wielebnowski 1999). As a result, it was suggested that providing ample access to hiding places, out of reach of disturbances, might

disproportionately benefit these individuals. Similarly, shy cuttlefish, who responded most passively and with the least threat behavior toward a predator, may require housing that shelters them from observers (Carere et al. 2015). Lastly, there is emerging empirical evidence to support such suggestions; for example, gorillas with high understanding scores seem to react more negatively to the presence of large crowds of visitors, as they performed more undesirable behaviors under these conditions, including stereotypes (Stoinski et al. 2012). Personality therefore has a large range of potential influences on the welfare animals experience, as well as our measures of it. Expanding our understanding of these effects can help us provide the animals under our care with the best possible welfare.

### **Learning and Problem Solving**

Personality has also been linked with individual variation in learning performance and problem solving, which is significant for several reasons. First, animal models are often used to inform our knowledge of the general mechanisms underlying learning and cognition. Ruling out any variation caused by confounding factors, such as personality, is therefore important for determining the true effects of experimental manipulations. Secondly, animal in many settings, such as pets, working roles, and veterinary check-ups, often need to be trained on specific behaviors. It is therefore useful to understand the influence of personality on training success, as this can facilitate the use of the most effective techniques for each individual.

The personality trait of exploration has been frequently assessed in relation to learning performance. For example, exploration types in rhesus macaques were associated with training success on a positive reinforcement task (Coleman et al. 2005). This type of training is commonly used in the management of captive populations. In this case, animals learned that a clicker sound was associated with being rewarded with a food treat from the trainer's hand. The monkeys then heard the clicker and received a reward if they touched a target hung outside their cage. Training was considered successful if over three consecutive 10 min sessions, the individual performed the

behavior on command at least 3 times. Exploratory monkeys, who approached and investigated novel food, were all successfully trained on the task, whereas only half of the individuals who never investigated the item were successfully trained.

Similar results have been found in other species. Ravens were assessed for their exploratory tendencies by measuring their latency to investigate a novel object, a bottle (Range et al. 2006). First, animals watched the experimenter place food inside a bottle. They were then given access to the bottle, which they had to manipulate to access the reward. More exploratory ravens were fastest at learning to solve this problem, primary due to initially approaching the bottle faster. Parallel results have been found in mice, in which more exploratory individuals were those who investigated more open areas in a novel environment (Matzel et al. 2003). Mice who exhibited this tendency also demonstrated more efficient learning on several different learning tasks: discriminating between rewarded and unrewarded odors, suppressing movement when exposed to an unpleasant stimulus, accuracy in locating a reward in a maze, and time taken to locate a hidden platform in a pool of water. One possible explanation for such findings is that exploratory individuals are simply more likely to encounter opportunities for learning, as they will be more likely to investigate novel environmental features (Sih et al. 2004).

Emerging evidence implicates other personality dimensions in specific aspects of learning abilities. In one study, rhesus macaques were trained on a serial chaining task, which requires a series of stimuli to be selected in the correct order. Initially, the item list is learnt by trial and error, with a food reward provided for a complete correct response (Altschul et al. 2016). Macaques rated as high on friendliness and openness personality dimensions exhibited lower error rates, and made better progress, meaning that they made it further through the list in the correct order before making an error or completing the sequence. More specifically, friendliness was associated with consistently better performance over time, while high openness was associated with faster rates of learning.

Finally, there is tentative research suggesting that certain personality types are associated with greater innovation and creativity, and therefore more efficient learning. Pigeons were assessed for neophobia, a common measure of the bold-shy axis, by measuring the time taken to feed when a novel object was placed next to their food dish (Bouchard et al. 2007). Birds who exhibited lower neophobia were more innovative in opening a problem box, thus facilitating faster task completion. These individuals also required fewer demonstrations by a conspecific to learn how to remove a stopper from a tube containing food, therefore exhibiting faster social learning. Bottlenose dolphins also show individual differences in the ability to mentally plan their behavior, leading to differences in the extent of trial and error required to solve problems (Kuczaj and Walker 2006; Kuczaj et al. 2009). Furthermore, the behavior of bold dolphins is more likely to be copied by other individuals (Kuczaj et al. 2006; Kuczaj and Yeater 2006). This is particularly interesting, as it suggests that differences in learning and problem-solving abilities may not only be related to one's own personality but also to that of those around you.

### Friendships

Like humans, members of many other species have friends. Unfortunately, we cannot ask a chimpanzee who they are friends with, but we can measure who they choose to spend time with and what they do during this time (Weinsten and Capitanio 2008). Personality seems to influence who become friends in the first place, and potentially one's satisfaction with these relationships over time. In rhesus macaques, affiliative behaviors tend to be performed most between related individuals of the same age and sex. However, when these factors were taken into account, individuals initiating affiliative behaviors with each other tended to have similar scores on two personality dimensions: adaptability and equitability (Weinsten & Capitanio 2008). Similarly, even when sex and age effects were accounted for, chimpanzee friends tended to have similar sociability scores (Massen and Koski 2014). In this study, the chimpanzee sociability personality

dimension contains descriptors such as many animals sitting close by, and the frequency of grooming received and given, both of which are known affiliative behaviors. Chimpanzee sociability has significant parallels with human extraversion (Goldberg 1990), which human friends also tend to score similarly on (Nelson et al. 2011). Another primate study also found support for this extraversion-friendship link, with capuchin pairs demonstrating higher quality relationships if they had similar sociability scores (Morton et al. 2015).

Although research examining links between animal friendships and personality has predominantly focused on primate species, it is likely that similar associations are present in other taxa. For example, recent evidence demonstrated that three personality factors – extraversion, conscientiousness, and neuroticism – influence the quality of bonds formed between pairs of bottlenose dolphins (Moreno 2017). Dolphins had the most positive bonds when each individual in a pairing scored similarly on the conscientiousness factor. This parallels the role of conscientiousness in human relationships; both teenager friendship quality (Jensen-Campbell and Malcolm 2007) and adult friendship satisfaction (Wilson et al. 2015) are associated with conscientiousness scores. Interestingly, the opposite pattern was true for extraversion and neuroticism. Pairs of dolphins who were dissimilar in their scores on these personality dimensions had the most positive bonds (Moreno 2017). Both similar and dissimilar extraversion scores have been associated with human friendships during college (Nelson et al. 2011), suggesting that bottlenose dolphin friendships may have specific features that facilitate dissimilar scores to a greater extent. The association between dissimilar neuroticism scores and dolphin bond quality (Moreno 2017) contrasts with findings in capuchins, in which relationships were more friendly and affiliative between individuals who were similar in neuroticism (Morton et al. 2015).

The maintenance of friendships over time may also be affected to some extent by personality. For example, not all rhesus macaque friendships are maintained in the long-term. The more similar

friends' equitability scores were at 1 year old, the greater the likelihood of those macaques still being friends 1 year later (Weinstein and Capitanio 2012). However, current evidence suggests that personality similarity or dissimilarity may be most important in the forming of friendships and then that other factors may become more important over time. This is consistent with findings in humans, in which personality has a greater effect on the formation of friendships, compared to their maintenance over time (Hartup 1996; Nelson et al. 2011).

### Human Disturbance

Personality may influence the extent to which individual animals are affected by human activities, such as wildlife tourism and urbanization. Firstly, while the former provides the potential for educating people about the natural environment, the public's high demand for this access to wildlife exposes animals to far greater levels of human disturbance than ever before. It has been suggested that individuals differ in their tolerance of these anthropogenic disturbances (Bejder et al. 2009). Depending on this tolerance level, some animals may suffer more severe consequences than others. For example, more sensitive animals may be immediately displaced upon the onset of human presence, while others may remain in the location. However, even those who remain may have personality characteristics that alter their behavioral reactions. Some animals seem to habituate to human presence, meaning that over time their response to humans decreases, whereas others become sensitized and exhibit more extreme behavior each time they are disturbed (Bejder et al. 2009). Furthermore, once human presence is no longer novel, it is difficult to assess the extent of our impact, as animals with low tolerance levels have already been displaced.

An empirical example of the effects of personality on initial response and subsequent habituation to human disturbance comes from yellow-eyed penguins. This species is endangered and found only in its home country of New Zealand (Ellenberg et al. 2009). Penguins were categorized into three personality types based on their response to a person in close proximity: timid,

calm, and aggressive. Each penguin was then assessed for habituation to human disturbance over five days, during which an experimenter approached the nest once per day. On the first day, the heart rates of calm and timid females took the longest time to return to baseline levels after human approach. Over the duration of testing, there was negligible change in the heart rate recovery time of aggressive birds. However, for calm birds, both recovery time and the maximum heart rate induced by the disturbance decreased. This reduction in reaction across repeated exposure indicates that habituation to human disturbance occurred only in birds with calm personalities. Such findings are of great importance for understanding the impact of well-meaning wildlife tourists, particularly for severely threatened species.

Not all sources of potential disturbance by humans come from tourism. Indeed, increased urbanization has the clear side effect of impacting animal populations. This provides the potential for benefits, such as new food sources and warmer temperatures, but also costs, such as increased potential for exposure to urban predators (Sol et al. 2013). Not all animals are equally suited for expanding into these urban environments, and it has been suggested that those of certain personality types, such as exploratory and bold, are most likely to reach more distant habitats and/or arrive first in a new habitat (Sol et al. 2013).

In support of such suggestions, some differences have been found in the personalities of birds inhabiting rural versus urban environments. In one study, personality was assessed in house sparrows from four locations varying in their extent of urbanization (Bokony et al. 2012). The four traits measured – object neophobia, food neophobia, risk taking, and activity – formed one broader personality dimension in birds from the rural locations. In urban sparrows, food neophobia (avoidance of novel food) remained a separate trait. A potential explanation for this finding is that sparrows inhabiting urban locations may have more food sources to choose from, thus relaxing the selection pressure experienced by rural birds. There were also more birds in the urban sample exhibiting very avoidant responses

in the predator test. This may represent an advantageous adaptation, due to their increased exposure to one of their predators, the sparrowhawk.

Negative features experienced within urban environments also do not seem to have the same effects on all personality types. In great tits, parents altered their nesting behavior in response to anthropogenic noise differently depending on their personality (Naguib et al. 2013). Parents of both sexes took longer to enter nest-boxes while urban background noise was played, and sex-dependent effects were also found; when noises were played, bold, fast-exploring females and shy, less-exploratory males reduced the frequency of visits to their nest-boxes. Such findings emphasize the complex relationships between anthropogenic impacts, personality, and a range of other factors. As our impact on the natural world increases, it is important to consider the characteristics of nonhuman animals at each level: species, population, and individual.

## Conclusion

Aside from being an interesting topic of research in its own right, the study of animal personality has far reaching implications and applications. For example, for pet owners, whether a new addition will assimilate well into the existing pack can often be a concern. Perhaps by knowing about the personality of your pets, you could maximize their chances of making friends. On a more serious note, there are millions of animals under human care around the world (Mason and Latham 2004), from pets, to zoo and aquarium animals, to research subjects. We therefore have a responsibility to provide these animals with the best possible level of care. As has been discussed here, personality has been linked with common measures of poor welfare, such as both the presence and absence of stereotypic behaviors (Mason and Latham 2004). Traits such as exploration (Range et al. 2006) and boldness (Bouchard et al. 2007) have also been associated with success in training animals on various learning tasks, which can be used to provide animals with individualized attention. Finally, increasing our knowledge of the

differential impacts of human presence on animals with varying personalities can benefit both our own interactions with the natural world and the well-being of the animals we live alongside.

## Cross-References

- ▶ [Animal Welfare](#)
- ▶ [Temperament](#)

## References

- Altschul, D. M., Terrace, H. S., & Weiss, A. (2016). Serial cognition and personality in macaques. *Animal Behavior and Cognition*, 3, 46–64.
- Bejder, L., Samuels, A., Whitehead, H., Finn, H., & Allen, S. (2009). Impact assessment research: Use and misuse of habituation, sensitisation and tolerance in describing wildlife responses to anthropogenic stimuli. *Marine Ecology Progress Series*, 395, 177–185.
- Bokony, V., Kulcsar, A., Toth, Z., & Liker, A. (2012). Personality traits and behavioral syndromes in differently urbanized populations of house sparrows (*Passer domesticus*). *PloS One*, 7(5), e36639.
- Bouchard, J., Goodyer, W., & Lefebvre, L. (2007). Social learning and innovation are positively correlated in pigeons (*Columba livia*). *Animal Cognition*, 10, 259–266.
- Carere, C., Grignani, G., Bonanni, R., Della Gala, M., Carlini, A., Angeletti, D., Cimmaruta, R., Nascetti, G., & Mather, J. (2015). Consistent individual differences in the behavioural responsiveness of adult male cuttlefish (*Sepia officinalis*). *Applied Animal Behaviour Science*, 167, 89–95.
- Coleman, K., Tully, L., & McMillan, J. (2005). Temperament correlates with training success in adult rhesus macaques. *American Journal of Primatology*, 65(1), 63–71.
- Connor, R. C., Wells, R. S., Mann, J., & Read, A. J. (2000). The bottlenose dolphin: Social relationships in a fission-fusion society. In J. Mann, R. C. Connor, P. L. Tyack, & H. Whitehead (Eds.), *Cetacean societies: Field studies of dolphins and whales* (pp. 91–126). Chicago: The University of Chicago Press.
- Cussen, V. A. (2013). *Personality and cognition in orange-winged Amazon parrots (Amazona amazonica): Implications for abnormal behavior and welfare* (ProQuest dissertations and theses). University of California, Davis.
- de Vere, A. J. (2017). *Do pinnipeds have personality? Coding harbor seal (Phoca vitulina) and California sea lion (Zalophus californianus) behavior across contexts* (ProQuest dissertations and theses). University of Southern Mississippi, Hattiesburg.
- Ellenberg, U., Mattern, T., & Seddon, P. J. (2009). Habituation potential of yellow-eyed penguins depends on sex, character and previous experience with humans. *Animal Behaviour*, 77(2), 289–296.
- Freeman, H., Gosling, S. D., & Schapiro, S. J. (2011). Methods for assessing personality in non-human primates. In A. Weiss, J. King, & L. Murray (Eds.), *Personality and behavioral syndromes in nonhuman primates* (pp. 17–41). New York: Springer.
- Gartner, M. C., & Powell, D. (2012). Personality assessment in snow leopards (*Uncia uncia*). *Zoo Biology*, 31, 151–165.
- Goldberg, L. R. (1990). An alternative “description of personality”: The big-five factor structure. *Journal of Personality and Social Psychology*, 59, 1216–1229.
- Gosling, S. D. (2001). From mice to men: What can we learn about personality from animal research? *Psychological Bulletin*, 127, 45–86.
- Gosling, S. D., & John, O. P. (1999). Personality dimensions in non-human species: A cross-species review. *Current Directions in Psychological Science*, 8, 69–75.
- Hartup, W. W. (1996). The company they keep: Friendships and their developmental significance. *Child Development*, 67, 1–13.
- Herrelko, E. S., Vick, S. J., & Auchanan-Smith, H. M. (2012). Cognitive research in zoo-housed chimpanzees: Influence of personality and impact on welfare. *American Journal of Primatology*, 74, 828–840.
- Highfill, L. E., & Kuczaj, S. A. (2007). Do bottlenose dolphins (*Tursiops truncatus*) have distinct and stable personalities? *Aquatic Mammals*, 33, 380–389.
- Ijichi, C., Collins, L., Creighton, E., & Elwood, R. (2013). Harnessing the power of personality assessment: Subjective assessment predicts behaviour in horses. *Behavioural Processes*, 96, 47–52.
- Jensen-Campbell, L. A., & Malcolm, K. T. (2007). The importance of conscientiousness in adolescent interpersonal relationships. *Personality and Social Psychology Bulletin*, 33(3), 368–383.
- Kuczaj, S. A., & Walker, R. T. (2006). How do dolphins solve problems. In E. A. Wasserman & T. R. Zentall (Eds.), *Comparative cognition: Experimental explorations of animal intelligence* (pp. 580–600). New York: Oxford University Press.
- Kuczaj, S. A., & Yeater, D. B. (2006). Dolphin imitation: Who, what, when, and why? *Aquatic Mammals*, 32, 413–422.
- Kuczaj, S. A., Makecha, R., Trone, M., Paulos, R. D., & Ramos, J. A. (2006). Role of peers in cultural innovation and cultural transmission: Evidence from the play of dolphin calves. *International Journal of Comparative Psychology*, 19, 223–240.
- Kuczaj, S. A., Gory, J. D., & Xitco, M. J. (2009). How intelligent are dolphins? A partial answer based on their ability to plan their behavior when confronted with novel problems. *The Japanese Journal of Animal Psychology*, 59, 99–115.



- Kulpa-Eddy, J., Taylor, S., & Adams, K. (2005). USDA perspective on environmental enrichment for animals. *ILAR Journal*, 46(2), 83–94.
- Lloyd, A. S., Martin, J. E., Bornett-Gauci, H. L. I., & Wilkinson, R. G. (2007). Evaluation of a novel method of horse personality assessment: Rater-agreement and links to behaviour. *Applied Animal Behaviour Science*, 105(1), 205–222.
- Mason, G. J., & Latham, N. R. (2004). Can't stop, won't stop: Is stereotypy a reliable animal welfare indicator? *Animal Welfare*, 13, 57–69.
- Massen, J. M., & Koski, S. E. (2014). Chimps of a feather sit together: Chimpanzee friendships are based on homophily in personality. *Evolution and Human Behavior*, 35, 1–8.
- Matzel, L. D., Han, Y. R., Grossman, H., Karnik, M. S., Patel, D., Scott, N., et al. (2003). Individual differences in the expression of a “general” learning ability in mice. *The Journal of Neuroscience*, 23, 6423–6433.
- Moreno, K. R. (2017). *Does personality similarity in bottlenose dolphin pairs influence dyadic bond characteristics?* (ProQuest dissertations and theses). University of Southern Mississippi, Hattiesburg.
- Morton, F. B., Weiss, A., Buchanan-Smith, H. M., & Lee, P. C. (2015). Capuchin monkeys with similar personalities have higher-quality relationships independent of age, sex, kinship and rank. *Animal Behaviour*, 105, 163–171.
- Naguib, M., vanOers, K., Braakhuis, A., & Waas, J. R. (2013). Noise annoys: Effects of noise on breeding great tits depend on personality but not on noise characteristics. *Animal Behaviour*, 85(5), 949–956.
- Nelson, P. A., Thorne, A., & Shapiro, L. A. (2011). I'm outgoing and she's reserved: The reciprocal dynamics of personality in close friendships in young adulthood. *Journal of Personality*, 79, 1113–1148.
- Range, F., Bugnyar, T., Schölgl, C., & Kotrschal, K. (2006). Individual and sex differences in learning abilities of ravens. *Behavioural Processes*, 73, 100–106.
- Reamer, L., Haller, R., Thiele, E., Freeman, H., Lambeth, S., & Schapiro, S. (2014). Factors affecting initial training success of blood glucose testing in captive chimpanzees (*Pan troglodytes*). *Zoo Biology*, 33, 212–220.
- Roberts, B. W., Walton, K. E., & Viechtbauer, W. (2006). Patterns of mean-level change in personality traits across the life course: A meta-analysis of longitudinal studies. *Psychological Bulletin*, 132(1), 1–25.
- Sih, A., Bell, A. A., & Johnson, J. C. (2004). Behavioural syndromes: An ecological and evolutionary overview. *Trends in Ecology & Evolution*, 19, 372–377.
- Sol, D., Lapedra, O., & Gonzalez-Lagos, C. (2013). Behavioral adjustments for life in the city. *Animal Behaviour*, 85(5), 1101–1112.
- Stoinski, T. S., Jaicks, H. F., & Drayton, L. A. (2012). Visitor effects on the behavior of captive western lowland gorillas: The importance of individual differences in examining welfare: Visitor effects on gorilla behaviour. *Zoo Biology*, 31, 586–599.
- Thomas, A., & Chess, S. (1977). *Temperament and development*. New York: Brunner/Mazel.
- Vandeleest, J. J., McCowan, B., & Capitanio, J. P. (2011). Early rearing interacts with temperament and housing to influence the risk for motor stereotypy in rhesus monkeys (*Macaca mulatta*). *Applied Animal Behaviour Science*, 132, 81–89.
- Watanabe, N. M., Stahlman, W. D., Blaisdell, A. P., Garlick, D., Fast, C. D., & Blumstein, D. T. (2012). Quantifying personality in the terrestrial hermit crab: Different measures, different inferences. *Behavioral Processes*, 91(2), 133–140.
- Weinstein, T. A., & Capitanio, J. P. (2008). Individual differences in infant temperament predict social relationships of yearling rhesus monkeys, (*Macacamulatta*). *Animal Behaviour*, 76, 455–465.
- Weinstein, T. A., & Capitanio, J. P. (2012). Longitudinal stability of friendships in rhesus monkeys (*Macacamulatta*): Individual- and relationship-level effects. *Journal of Comparative Psychology*, 126, 97–108.
- Weiss, A., & Adams, M. J. (2013). Differential behavioral ecology. In C. Carere & D. Maestriperi (Eds.), *Animal personalities: Behavior, physiology and evolution*. Chicago: University of Chicago Press.
- Wielebnowski, N. C. (1999). Behavioral differences as predictors of breeding status in captive cheetahs. *Zoo Biology*, 18, 335–349.
- Wilson, R. E., Harris, K., & Vazire, S. (2015). Personality and friendship satisfaction in daily life: Do everyday social interactions account for individual differences in friendship satisfaction? *European Journal of Personality*, 29(2), 173–186.
- Yamanashi, Y., & Matsuzawa, T. (2010). Emotional consequences when chimpanzees (*Pan troglodytes*) face challenges: Individual differences in self-directed behaviors during cognitive tasks. *Animal Welfare*, 19, 25–30.



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### Introduction

The renaissance period of animal cognition in the early 1970s (Hulse et al. 1978) witnessed the emergence of several notable figures that championed an effort to describe the cognitive characteristics (i.e., abilities, specializations and limitations) of different species. Louis M. Herman was among these pioneers whose findings ushered in a new view of animal cognition that extended beyond the restrictive stimulus-response lens of the past. Considered by many to be the “father” of dolphin cognition, Dr. Herman spent nearly 50 years with his many students and colleagues conducting groundbreaking studies that revealed the remarkable cognitive capacity of bottlenose dolphins (*Tursiops truncatus*). In parallel with these efforts, he pioneered the scientific study of humpback whales (*Megaptera novaeangliae*) in Hawaiian waters. The marine mammal laboratory Dr. Herman created became world renowned not only for its scientific studies and breakthroughs in the study of dolphin cognition and whale behavior but also for the unique applied learning opportunities it provided to students of all ages through

volunteer apprenticeship programs, college-level internships, and higher level degree programs. On August 3, 2016, after five decades of research and publishing about dolphins and whales, Dr. Herman passed away. Full biographies of Dr. Herman’s life and remarkable career in marine mammal science can be found in Herman (2012) and Pack et al. (2017).

### Background, Education, and Early Career Directions

Louis M. Herman was born in Queens, New York, in 1930. He earned his bachelor’s and master’s degrees in Psychology at City College of New York. After serving as an intelligence officer in the US Air Force and studying concept learning in rhesus monkeys at Emory University in Atlanta, Georgia, Dr. Herman entered the doctoral program at Pennsylvania State University where he investigated human information processing. His dissertation, awarded in 1961, explored how humans process information when confronted with competing cognitive demands from two simultaneous auditory tasks. The American Institutes for Research honored Dr. Herman’s work with first prize in their inaugural “Creative Talent Award” in Psychology. In their citation of Dr. Herman’s work, eminent psychologists Harry Harlow, James Miller, and Theodore Newcomb wrote “This thesis, beautifully conceived and executed, displays a wealth of knowledge and

historical documentation on a modern problem of great significance in psychology” (Harlow et al. 1962, p. 681). Dr. Herman continued his studies of human information processing and performance at North American Aviation in Columbus, Ohio, from 1961 to 1963 and at Queens College in New York City as an assistant professor from 1963 to 1966 (see Pack et al. 2017 for references to some of these studies). In 1966, he joined the Psychology Department at the University of Hawaii at Manoa where he remained for the rest of his career. In his personal life, he was an avid long distance ocean swimmer and most importantly a devoted husband and father to his wife Hannah and their daughter Elia.

### **Founding the First Laboratory Fully Devoted to Dolphin Cognition**

When he joined the University of Hawaii, Dr. Herman’s research plans were to continue his studies with humans; however, his attention was soon diverted to another large-brained social mammal, the bottlenose dolphin, whose cognitive capacities he realized had received surprisingly little scientific investigation (see Herman 2012 for examples of some early work). An intriguing summer study on dolphin rule learning at Hawaii’s Sea Life Park in 1967 serendipitously turned into an opportunity to have dolphin pupils at a laboratory of his own creation that could be fully devoted to the study of dolphin sensory perception, cognition, and language comprehension. In 1969, after locating and converting an abandoned shark display facility to house dolphins, Dr. Herman launched the Kewalo Basin Marine Mammal Laboratory (KBMML). There, together with his dolphin pupils (Keakiko, Nana, Puka, Akeakamai, Phoenix, Hiapo, and Elele), 38 graduate students, and scores of undergraduates, he produced numerous groundbreaking studies in dolphin cognition and humpback whale behavior. Following the close of KBMML in 2004, Dr. Herman continued his innovative studies of humpback whale behavior until his passing (summarized in Herman 2016).

### **Dolphin Sensory Perception and Cross-Modal Abilities**

Recognizing that little was known about dolphin sensory perception, Dr. Herman’s earliest studies at KBMML explored dolphin hearing and vision as a foundation for future inquiries into dolphin cognition. Starting with dolphin hearing, Dr. Herman demonstrated the dolphin’s ability to detect small degrees of frequency modulation and its sensitivity to other types of sounds as well as temporal differences in sounds (summarized in Herman 1980b). Dr. Herman next tackled dolphin vision, performing pioneering studies of dolphin visual acuity that showed that dolphins see well (about 8–12 min of arc) both in air and underwater (Herman et al. 1975). He also explored the dolphin’s sensitivity in different areas of the visible spectrum and characterized its limitations in discriminating different colors (Madsen and Herman 1980). Much later, Dr. Herman and his students revealed that dolphins could immediately recognize complexly shaped objects across echolocation and vision (Herman et al. 1998; see also summary in Pack et al. 2004). For the latter work, Dr. Herman and his coauthors received the American Psychological Association Division 6’s F.A. Beach Comparative Psychology Award for best paper published in the *Journal of Comparative Psychology* in 1998.

### **Dolphin Rule Learning and Concept Formation**

In the 1970s, Dr. Herman began investigating the efficiency with which dolphins could acquire and apply generalized rules and concepts, in keeping with other animal cognition studies of the times. His work with learning sets showed that dolphins could learn and apply a “win-stay, lose-shift” rule across numerous novel problems after a single trial with arbitrary sounds and also that they could immediately shift response strategies within problems after reward contingencies were reversed. They performed both of these tasks at levels comparable to what had been shown with nonhuman primates (Herman 1980b). Dr. Herman

and his students also investigated the dolphin's ability to develop a concept of same/different and apply this to novel problems in different modalities. Using matching-to-sample (MTS) tasks as well as tasks involving symbolic judgments of similarity and difference using either simultaneously presented stimuli or successively presented stimuli, the dolphins performed accurately on first trials across numerous problems with novel auditory and visual materials (Herman 1980b; Herman et al. 1993b; Mercado et al. 2000). With one dolphin, acquisition of the same/different concept was near instantaneous suggesting that when confronted with tasks requiring judgments of similarity and difference, dolphins, like chimpanzees, may be predisposed toward cognitive solutions involving concepts rather than memorizing stimulus-specific rote associations (Herman et al. 1993b). Finally, in the mid-1990s, Dr. Herman and his students began to investigate the types of mental representations of objects dolphins formed through echolocation. The results of these studies revealed that complexly shaped objects inspected by the dolphin through echolocation were represented holistically rather than through individual features. They also showed that objects that had never previously been experienced simultaneously through echolocation and vision, as well as novel objects, could be matched across these senses (summarized in Pack et al. 2004). Collectively, these studies demonstrated that dolphins can abstract a same/different concept from relatively few exemplars and can readily apply that concept on first trials across numerous pairs of novel stimuli in different modalities and even across the senses at levels comparable to those demonstrated with some non-human primates.

### **Dolphin Memory Abilities and Processes**

In the 1970s, recognizing that memory is the bedrock upon which all cognition rests, Dr. Herman and his students also investigated for the first time dolphin short-term memory abilities and processes. Early work is summarized in Herman (1980b). In studies of auditory MTS in which

various delays were interposed between the offset of the sample sound and onset of the alternative sounds, Dr. Herman showed that matching accuracy remained at or near ceiling levels across hundreds of pairs of novel sounds for nearly all delays tested up to 120 sec (the longest delay tested), a finding comparable to what has been found in several species of nonhuman primates (Herman 1980b). He also showed that like visual short-term memory in primates, short-term memory for sounds in MTS tasks was subject to both proactive interference (i.e., interference from earlier experienced sounds on the memory of later sounds), as well as retroactive interference (i.e., interference from noise inserted during the delay period on the memory of sounds experienced prior to the delay). In some of the first serial-probe-recognition tasks run with animals, in which a list of sounds was followed by a probe sound which the dolphin judged symbolically as either on or absent from the list, Dr. Herman showed that memory span for lists of novel sounds was between four and five sounds. He also demonstrated a recency effect with increasing list length, as had been shown in humans and nonhuman primates. Later, Dr. Herman and his students extended these studies by demonstrating that short-term memory retention abilities for various types of visual materials were comparable to those witnessed with auditory materials and that the dolphin was also capable of maintaining representations of motor behaviors either performed by another dolphin or behaviors that were self-performed (Herman et al. 1993b; Herman 2002). In a unique variant of the latter task, Dr. Herman and his students taught a dolphin to respond to a "repeat" command by repeating the last behavior it performed and also to an "any" command by performing any one of five behaviors except the one that it last performed. The dolphin was tested on different sequences of four commands. Each sequence began with a command to perform a specific behavior. The next three gestures were different combinations of "any" and "repeat." The dolphin performed with high accuracy, including on those trials in which it was required to repeat self-selected behaviors (Herman 2002). The dolphin's ability to correctly carry out these

sequences demonstrated important aspects of the management of working memory including maintaining, monitoring, and updating mental representations. Collectively, these studies showed that dolphins have well-developed short-term memory capabilities and working memory processes that can flexibly handle material in different modalities and which are critical for supporting higher-level cognitive tasks.

### **Dolphin Imitative Abilities**

In many ways, Dr. Herman was ahead of his time in terms of recognizing the significance of particular aspects of animal cognition. For example, prior to a renewed interest in animal imitation and the recognition of its complexity and importance in social learning in the 1990s, Dr. Herman and his students had already conducted groundbreaking laboratory studies of imitation in dolphins, who in the wild demonstrate a natural ability to copy the signature whistles of close companions and closely coordinate similar behaviors with these individuals (Herman 2002). They showed for the first time that a dolphin could imitate with high fidelity a variety of arbitrary computer-generated familiar and novel sounds (Richards et al. 1984) and also that it could imitate a variety of familiar and novel arbitrary behaviors produced by either another dolphin or by a human (either in the dolphin's habitat or at tank-side or displayed on a small television monitor placed behind an underwater window) (Herman 2002). The ability of the dolphin to imitate both novel sounds and motor behaviors, and to respond to an "imitate" signal (in contrast to other signaled commands), demonstrated that it could develop a broad and generalized concept of imitation thus far unmatched in studies with other nonhuman animals.

### **Studies of Dolphin Social Awareness and Self-Awareness**

In the 1990s, Dr. Herman and his students began to investigate forms of social awareness beyond

imitation. These studies focused on the management of joint attention between an informant and a receiver toward objects of interest by testing the dolphins' understanding of human pointing and/or gazing. Joint attention is recognized as an essential component of social cognition (Pack and Herman 2006). Early work with nonhuman primates showed that they had difficulty in comprehending pointing cues, unless the tip of the informant's pointing finger was positioned nearly touching a focal object (reviewed in Pack and Herman 2006). In contrast, Herman et al. (1999) demonstrated that dolphins could respond accurately on first trials to dynamic brief human pointing cues toward distal objects including those placed behind the dolphin. The dolphin could also immediately understand sequences of pointing cues when these were substituted for gestural references to objects that instructed the dolphin to create relationships between two objects (see section on sentence comprehension below). Later work extended these discoveries by demonstrating that dolphins could immediately understand static human pointing cues as well as both static and dynamic human gazing cues at objects (Pack and Herman 2006). Together, these studies showed that the dolphins understood the referring function of pointing and gazing, and they complemented other work performed at Epcot's Living Seas facility in Florida by some of Dr. Herman's former students and colleagues showing dolphins spontaneously producing pointing behaviors (by aligning their rostrum and body toward an object) and understanding the importance of attentiveness of a receiver (reviewed in Pack and Herman 2006). Dr. Herman and his students also studied various forms of self-awareness. They showed that a dolphin could on command recall its own actions including those behaviors of its own choosing or creation (summarized in Herman 2002). They also showed that a dolphin could both understand human-directed references to its own body parts and could use referenced body parts in different ways (e.g., to touch or toss an object) (Herman et al. 2001). This work adds to the understanding of dolphin self-awareness, which has also been demonstrated in

mirror self-recognition studies (Reiss and Marino 2001).

### **Studies of the Interpretation of Television Displays**

One of the most unexpected and remarkable abilities shown in dolphins by Dr. Herman was their capacity to spontaneously (i.e., without training) understand television displays as representations of the real world. When confronted for the first time with the small, 20 cm image of a trainer on a television monitor placed behind an underwater window in their habitat, both the dolphins Phoenix and Akeakamai (Ake) immediately understood gestural signs given by this trainer including, for Ake, imperative sentences within her language (see section below on sentence comprehension) (Herman et al. 1990). The immediacy with which the dolphins interpreted these television displays as representations of the real world stands in contrast to the initial difficulty common chimpanzees had with this understanding (Savage-Rumbaugh 1986). In addition to understanding the gestural signs from the small image of a trainer, the dolphins also understood gestural signs that were reduced to point-light displays (i.e., points of light against a black background moving about in place of the trainers arms and hands) (Herman et al. 1990). Further studies showed that they also understood the relationship between a small, televised image of an object and the same real-sized object inspected through echolocation (Pack et al. 2004), and could imitate televised behaviors of a human (Herman et al. 1993b; Herman 2002).

### **Studies of Comprehension of Sentences by Dolphins**

Arguably, the most notable of Dr. Herman's contributions to the field of animal cognition have been in language comprehension (Herman 1986, 1987, Herman and Forestell 1985; Herman et al. 1984, 1993a,b). Dr. Herman created two artificial language systems in which either human-

generated gestural signals (taught to Ake) or computer-generated acoustic signals (taught to Phoenix) were used to express individual "words" in various semantic categories (agents, objects, actions, modifiers, relationships). Sequences of words were used to compose sentences up to five words in length according to various syntactic frames and constraints. A "sentence" was defined as "a sequence of words that expressed a unique semantic proposition" (Herman et al. 1984, p. 135) and was given in the imperative or interrogative mode. Imperatives required the dolphin to take named actions to named objects taking into account their named modifiers or asked the dolphin to construct a relationship between two named objects. To illustrate the complexity of some of the imperatives, the five-word relational sentence *Right Hoop Left Ball Fetch* asked Ake to take the ball on her left to the hoop on her right, with pairs of hoops and balls present as well as other named objects. The modifiers *Left* and *Right* could exchange positions in the sentence as could the objects *Hoop* and *Ball*, and the relationship term *In/On* could be exchanged for the relationship term *Fetch* to create a variety of new instructions, all of which Ake understood. The findings (see earlier citations) established the ability of Phoenix and Ake to take account of both the semantic and syntactic features of their separate language systems to carry out the instructions embedded in the sentences. Among other things, the dolphins could understand instructions new to their experience, derive the meaning of new syntactic frames that were extensions of existing frames, understand the different meanings of novel sentences in which the same words were placed in different orders, decode semantically or syntactically anomalous sentences, and immediately generalize the lexical references to objects to include different exemplars of those objects. The only other nonhuman species that has shown similar capabilities for comprehension of novel sentences using a variety of objects and in different contexts is the Bonobo (*Pan paniscus*) (Savage-Rumbaugh et al. 1993). In addition to understanding imperative sentences, Ake could report accurately (by responding on *yes* or *no* paddles) whether a named object was present in

or absent from her habitat (interrogative sentences). For example, the interrogative *Frisbee Question* asked whether the named object *Frisbee* was present or not in the dolphin's habitat. The ability of the dolphin to report that a symbolically referenced object was absent from the habitat as well as to understand the same symbol in a variety of different sentence types and contexts was strong evidence that language symbols were understood referentially (Herman and Forestell 1985; Herman et al. 1993b).

### Field Studies of Humpback Whale Behavior

The multitude of diverse and innovative studies described above could alone characterize a remarkable career. However, as noted earlier, Dr. Herman was also prolific in the studies he and his students conducted on humpback whale behavior in their Hawaiian breeding grounds and Alaskan feeding grounds. In 1976, when most people were unaware of the presence of humpback whales in Hawaiian waters, Dr. Herman pioneered their scientific study with the first aerial and boat-based surveys of their numbers, association patterns, and habitat use (see Herman 2012). He then created one of the longest continuous field studies of the behavioral ecology of humpback whales ever conducted and through this was able to trace the life histories of individual whales for over 30 years (Herman et al. 2011). The work of Dr. Herman and his students produced a wealth of new information on humpback whale behavior, which Dr. Herman summarized in his final publication on humpback whales produced in the last year of his life (Herman 2016). Some of these findings were the description of the behavioral role and coining of the term "escort" to describe the whale(s) accompanying a mother-calf pair; that males demonstrate mate guarding in the breeding grounds; that male-male competition over single females in the breeding grounds can escalate from dramatic displays to blood-shedding fights; that male size confers an advantage in competition; that affiliations between humpback whales in the breeding grounds (other than

mother-calf pairs) are best characterized as transient; that playback of humpback whale song is much less attractive than playback of a feeding call in the breeding grounds (a finding that later served to help rescue "Humphrey the Wrong Way Whale" from San Francisco Bay in 1985); that males prefer to associate with females without calf (i.e., those with a higher reproductive potential), rather than females with calf (i.e., those with a lower reproductive potential); that across years, females vary their migratory timing depending on their reproductive status; that larger females produce larger calves and tend to attract greater numbers of male escorts than do smaller females; that mature females prefer associating with larger sized adult males; that females with calf tend to segregate into shallow water to avoid male harassment; that both mature and immature males sing in the breeding grounds; and that the mating system in humpback whales has the essential requisite characteristics of a lek mating system.

### Conclusions

Dr. Herman's collective works are documented in 181 scientific publications including two edited books (Herman 1980a; Roitblat et al. 1993). His discoveries have been featured nationally and internationally in over 230 newspaper and magazine articles, radio broadcasts, television documentaries, and IMAX films. At a point in history when much of animal cognition research was focused on rats, pigeons, and nonhuman primates, Dr. Herman's findings compelled researchers to take notice of the similarities in cognition between dolphins and apes despite their divergent evolutionary lines. Dr. Herman's genius was also in his creative approach to designing scientifically rigorous and unique methods to ask each research question of *dolphins* (in contrast to humans or nonhuman primates) and to continuously adapt his approach in response to the dolphins' behaviors. From the outset, Dr. Herman's goal was to describe dolphin cognition within a comparative framework and "to understand eventually the pressures selecting for intellect and how particular cognitive specializations are adaptive" (Herman



1980b, p. 364). Dr. Herman continued working diligently to reach this goal until his passing. His revelations reinforced his earliest ideas that aside from the dolphin's relatively large brain size, a major evolutionary impetus for the development of its broad, flexible, and sophisticated suite of higher cognitive skills appears to be the elaborate social matrix and communication network typical of wild dolphin societies in which cooperation and competition play roles, the strengths of individual relationships are constantly being assessed, and young calves enjoy a protracted period of parental care through which to observe and learn (Herman 1980b, 2006). In 2004, Dr. Herman was honored as an American Psychological Association's President's Program Featured Speaker, and in 2008, his work with dolphins as well as humpback whales was recognized among the top 100 pioneering accomplishments in the history of the University of Hawaii. Beyond these and many other accolades, Dr. Herman will always be remembered as a pioneer who led one of the most productive long-term field studies of any whale species and advanced the field of dolphin cognition from virtual ignorance to a well-established position in the history of animal cognition research.

## Cross-References

- ▶ [Brain Size](#)
- ▶ [Cetacean Cognition](#)
- ▶ [Cetacean Communication](#)
- ▶ [Cetacean Life History](#)
- ▶ [Cetacean Sensory Systems](#)
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- ▶ [Syntax](#)
- ▶ [Win-Stay](#)

## References

- Harlow, H. F., Miller, J. G., & Newcomb, T. M. (1962). Identifying creative talent in psychology. *The American Psychologist*, *17*, 679–683.
- Herman, L. M. (Ed.). (1980a). *Cetacean behavior: Mechanisms and functions*. New York: Wiley Interscience.
- Herman, L. M. (1980b). Cognitive characteristics of dolphins. In L. M. Herman (Ed.), *Cetacean behavior: Mechanisms and functions* (pp. 363–429). New York: Wiley Interscience.
- Herman, L. M. (1986). Cognition and language competencies of bottlenosed dolphins. In R. J. Schusterman, J. Thomas, & F. G. Wood (Eds.), *Dolphin cognition and behavior: A comparative approach* (pp. 221–251). Hillsdale: Lawrence Erlbaum Associates.
- Herman, L. M. (1987). Receptive competencies of language trained animals. In J. S. Rosenblatt, C. Beer, M. C. Busnel, & P. J. B. Slater (Eds.), *Advances in the study of behavior* (Vol. 17, pp. 1–60). Petaluma: Academic Press.
- Herman, L. M. (2002). Vocal, social, and self-imitation by bottlenosed dolphins. In C. Nehaniv & K. Dautenhahn (Eds.), *Imitation in animals and artifacts* (pp. 63–108). Cambridge, MA: MIT Press.
- Herman, L. M. (2006). Intelligence and rational behaviour in the bottlenosed dolphin. In S. Hurley & M. Nudds (Eds.), *Rational animals?* (pp. 439–467). Oxford: Oxford University Press.
- Herman, L. M. (2012). Historical perspectives. *Aquatic Mammals*, *38*, 102–125.
- Herman, L. M. (2016). The multiple functions of male song within the humpback whale (*Megaptera novaeangliae*)

- mating system: Review, evaluation, and synthesis. *Biological Reviews*. doi:10.1111/brv.12309.
- Herman, L. M., & Forestell, P. H. (1985). Reporting presence or absence of named objects by a language-trained dolphin. *Neuroscience and Biobehavioral Reviews*, *9*, 667–691.
- Herman, L. M., Peacock, M. F., Yunker, M. P., & Madsen, C. (1975). Bottlenosed dolphin: Double-slit pupil yields equivalent aerial and underwater diurnal acuity. *Science*, *139*, 650–652.
- Herman, L. M., Richards, D. G., & Wolz, J. P. (1984). Comprehension of sentences by bottlenosed dolphins. *Cognition*, *16*, 129–219.
- Herman, L. M., Morrel-Samuels, P., & Pack, A. A. (1990). Bottlenosed dolphin and human recognition of veridical and degraded video displays of an artificial gestural language. *Journal of Experimental Psychology: General*, *119*, 215–230.
- Herman, L. M., Kuczaj III, S., & Holder, M. D. (1993a). Responses to anomalous gestural sequences by a language-trained dolphin: Evidence for processing of semantic relations and syntactic information. *Journal of Experimental Psychology: General*, *122*, 184–194.
- Herman, L. M., Pack, A. A., & Morrel-Samuels, P. (1993b). Representational and conceptual skills of dolphins. In H. R. Roitblat, L. M. Herman, & P. Nachtigall (Eds.), *Language and communication: Comparative perspectives* (pp. 273–298). Hillsdale: Lawrence Erlbaum Associates.
- Herman, L. M., Pack, A. A., & Hoffmann-Kuhnt, M. (1998). Seeing through sound: Dolphins perceive the spatial structure of objects through echolocation. *Journal of Comparative Psychology*, *112*, 292–305.
- Herman, L. M., Abichandani, S. L., Elhaji, A. N., Herman, E. Y. K., Sanchez, J. L., & Pack, A. A. (1999). Dolphins (*Tursiops truncatus*) comprehend the referential character of the human pointing gesture. *Journal of Comparative Psychology*, *113*, 1–18.
- Herman, L. M., Matus, D. S., Herman, E. Y. K., Ivancic, M., & Pack, A. A. (2001). The bottlenosed dolphin's (*Tursiops truncatus*) understanding of gestures as symbolic representations of its body parts. *Animal Learning & Behavior*, *29*, 250–264.
- Herman, L. M., Pack, A. A., Rose, K., Craig, A., Herman, E. Y. K., Hakala, S., & Milette, A. (2011). Resightings of humpback whales in Hawaiian waters over spans of ten to 32 years: Site fidelity, sex ratios, calving rates, female demographics, and the dynamics of social and behavioural roles of individuals. *Marine Mammal Science*, *27*, 736–768.
- Hulse, S. H., Fowler, H., & Honig, W. K. (Eds.). (1978). *Cognitive processes in animal behavior*. Hillsdale: Lawrence Erlbaum Associates.
- Madsen, C. J., & Herman, L. M. (1980). Social and ecological correlates of vision and visual appearance. In L. M. Herman (Ed.), *Cetacean behavior: Mechanisms and functions* (pp. 101–147). Hillsdale: Wiley Interscience.
- Mercado III, E. M., Killebrew, D. A., Pack, A. A., Macha, I. V. B., & Herman, L. M. (2000). Generalization of same-different classification abilities in bottlenosed dolphins. *Behavioural Processes*, *50*, 79–94.
- Pack, A. A., & Herman, L. M. (2006). Dolphin social cognition and joint attention: Our current understanding. *Aquatic Mammals*, *32*, 443–460.
- Pack, A. A., Herman, L. M., & Hoffmann-Kuhnt, M. (2004). Dolphin echolocation shape perception: From sound to object. In J. Thomas, C. Moss, & M. Vater (Eds.), *Advances in the study of echolocation in bats and dolphins* (pp. 288–298). Chicago: University of Chicago Press.
- Pack, A. A., Herman, E. Y. K., Baker, C. S., Bauer, G. B., Clapham, P. J., Connor, R. C., Craig, A. S., Forestell, P. H., Frankel, A. S., Notarbartolo Di Sciara, G., Hoffmann-Kuhnt, M., Mercado III, E., Mobley, J., Shyan-Norwalt, M. R., Spitz, S. S., Solangi, M., Thompson, R. K. R., Uyeyama, R., Wells, R., & Wolz, J. P. (2017). Memories: Louis M. Herman 1930–2016. *Marine Mammal Science*, *33*, 389–406.
- Reiss, D., & Marino, L. (2001). Mirror self-recognition in the bottlenose dolphin: A case of cognitive convergence. *Proceedings of the National Academy of Science of the United States America*, *98*, 5937–5942.
- Richards, D. G., Wolz, J. P., & Herman, L. M. (1984). Vocal mimicry of computer generated sounds and vocal labeling of objects by a bottlenosed dolphin, *Tursiops truncatus*. *Journal of Comparative Psychology*, *98*, 10–28.
- Roitblat, H. R., Herman, L. M., & Nachtigall, P. (Eds.). (1993). *Language and communication: Comparative perspectives*. Hillsdale: Lawrence Erlbaum Associates.
- Savage-Rumbaugh, E. S. (1986). *Ape language: From conditioned response to symbol*. New York: Columbia University Press.
- Savage-Rumbaugh, E. S., Murphy, J., Sevcik, R. A., Brakke, K. E., Williams, S. L., & Rumbaugh, D. M. (1993). Language comprehension in ape and child. *Monographs of the Society for Research in Child*, *58*, 1–252.

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## John Bowlby

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### Introduction

John Bowlby is best known as the father of attachment theory. First developed in the 1950s, attachment theory was both shaped by and significantly influential on the study of animal behavior. This entry will describe Bowlby's biography as it relates to the development of attachment theory, the major principles of and significant influences on his theory, and its applications to animal research.

### Early Life

Edward (John) Mostyn Bowlby (1907–1990) was born in London, England, to an upper-middle class family. As was characteristic of the time, he and his five siblings were raised primarily by a series of nannies and nursemaids. Bowlby only visited with his mother for an hour each day and with his father considerably less. His first nursemaid, Minnie, served as a mother substitute for him, and when she left the family when Bowlby was four-years-old, it served as a devastating loss.

This would prove to be profoundly influential on his later research interests (Van Dijken 1998).

### Education and Clinical Experience

At the age of 11, Bowlby was sent to boarding school and at 14 entered the Royal Naval College, Dartmouth. In 1924, after spending less than a year training on a naval ship, Bowlby decided to leave the navy and pursue the study of medicine (Van Dijken 1998). He received his undergraduate degree from Trinity College at the University of Cambridge in 1928. While there, Bowlby recalled focusing a considerable amount of his time on evolutionary biology, which would prove influential on his development of attachment theory (Van Dijken 1998). He was also introduced to the field now known as developmental psychology, then in its nascence (Bretherton 1992). This persuaded him to leave his studies in medicine for psychology for the remainder of his undergraduate years. He would, however, return to the field to medicine, earning his degree from London's University College Hospital, in order to pursue a career in psychiatry. This was partially influenced by his work at a school for maladjusted children where he encountered children whose psychological problems appeared to be closely linked to their early childhood experiences of parental deprivation. Witnessing this association between early

familial relationships and later development solidified Bowlby's interests in child psychiatry (Bretherton 1992).

As Bowlby pursued his studies in medicine and psychiatry, he also began training in psychoanalysis at the British Psychoanalytic Institute. His supervisor, Melanie Klein, shared his interests in early relationships and the damaging effects of early loss. However, as was characteristic of the field at the time, Klein's focus was almost exclusively on unconscious processes, to the exclusion of examining the actual experiences of children. Bowlby rejected this premise and sought out to prove that real-world experiences of trauma and loss have the most powerful influence on personality development (Bretherton 1992). This was supported by his first empirical paper which traced the development of 44 juvenile thieves back to their history of early separation from their mothers and other adverse childhood experiences (Van Dijken 1998).

Following the completion of his psychiatric and psychoanalytic training, Bowlby was appointed head of the Children's Department at Tavistock Clinic, an organization focused on social and preventative psychiatry. It was here that attachment theory was first developed.

## Development of Attachment Theory

### Core Tenants of Attachment Theory

At its core, attachment theory argues that the parent-child relationship is critical for both the child's immediate survival and their long-term psychological well-being. In Bowlby's writings, this is traditionally described as the mother-child relationship although he acknowledged the role of "mother substitute" figures, perhaps harkening back to his own childhood experiences with his nursemaid. Bowlby's theory is based in both developmental psychology and ethology. He argued that the attachment relationship is built upon a series of instinctual behaviors designed to bond infants and mothers together in order to ensure that the vulnerable infant receives the care they need. This need for protection, and the depth of the bond formed, helps to explain why

infants demonstrate such significant separation anxiety when apart from their mothers and why long-term separation can have such devastating psychological consequences, as Bowlby observed in his studies of maladjusted children and juvenile thieves (Bowlby 1982; Bretherton 1992).

Bowlby defined attachment as a behavioral system, similar to but separate from mating or feeding, which has evolved to promote the survival and reproductive success of the individual. In the case of the attachment system, the infant is drawn to maintain proximity to their attachment figure (the person who is most responsive to the infant's needs for care). As the child develops, so does the attachment relationship, becoming what Bowlby described as "goal-corrected partnership" as the child becomes more attuned to their caregiver's psychological perspective. Bowlby also argued that children's experiences with their attachment figures become mentally represented via what are known as "internal working models" (IWMs) which are then used as a way to predict future interactions with relationship partners and the world in general (Bowlby 1982).

### Collaboration with Mary Ainsworth and the Assessment of Attachment

Several years after Bowlby's arrival at the Tavistock Clinic, a scientist by the name of Mary Ainsworth joined his research unit. It was Ainsworth who completed the first empirical study of attachment, observing 26 families with infants living in Uganda over a period of 9 months. It was here that Ainsworth first noted three distinct patterns of attachment-related behavior: babies who seemed content in the presence of their mothers and explored comfortably under her supervision (now classified as securely attached), those who cried frequently in her presence and explored little (insecure ambivalent), and those who showed little regard for whether or not their mother was present (insecure avoidant). Upon returning from Uganda, Ainsworth began a second observational study of 26 families in Baltimore where again Ainsworth was struck by the individual differences in how both infants and mothers responded to each other (Bretherton 1992). From this work, Ainsworth developed a

standardized laboratory procedure, the Strange Situation, which was designed to capture the quality of the infant-parent attachment relationship over the course of a 20-min observation (Ainsworth et al. 1978). The Strange Situation is still considered the gold standard for attachment assessments, and Ainsworth's empirical work helped to provide evidence in support of Bowlby's theory.

### **Ethological and Comparative Psychology Influences on Bowlby's Work**

Bowlby's theory of attachment was born out of his education and training in both developmental psychology (which, at the time, was heavily steeped in psychoanalytic theory) and evolutionary psychology. In taking an evolutionary approach to explain the origins of the attachment relationship among human parents and children, Bowlby recognized that this type of relationship was also likely to exist in our closest evolutionary kin. He was also interested in attachment-related behaviors, such as imprinting, which are present in other species. For example, Bowlby was drawn to Konrad Lorenz's research on imprinting in goslings, which demonstrated the critical role that the parent-child connection plays in promoting the survival of vulnerable young. Bowlby was also drawn to Lorenz and others' ethological approach, which requires the observation of animals in their natural environment, and was similar to Ainsworth's work in Uganda and Baltimore and other research being conducted at Tavistock (Bretherton 1992).

Although Bowlby favored an ethological approach to animal research, he was also deeply influenced by the work of Harry Harlow who used experimental methods to study affectional bonds in rhesus monkeys. Harlow was particularly interested in the effect of parental deprivation on infant monkeys. In 1957 Bowlby and Harlow began a written correspondence which eventually led Bowlby to visit Harlow's monkey laboratory at the University of Wisconsin. Bowlby often cited his observations at Harlow's lab in explaining the behavior of human infants, for example, linking pathological thumb sucking in children to the nonnutritive sucking behavior demonstrated by

monkeys who had been raised in isolation (van der Horst et al. 2008).

### **Contributions to the Study of Animal Behavior**

As Bowlby recognized, the attachment bond is not unique to the human species. This fact has long been supported by research with nonhuman primates, including chimpanzees and rhesus monkeys. It is worth noting, however, that attachment relationships are not universal across primates. Research on New World monkeys, such as capuchins, and prosimian species has demonstrated that they imprint on their mothers but do not form the complexity of an attachment bond (Suomi 2016).

The study of rhesus monkey attachment dates all the way back to the 1950s with Harry Harlow. Just as Harlow's work was influential on Bowlby as he developed attachment theory, so was Bowlby's new theory influential on Harlow's subsequent research. For example, in a series of experiments, Harlow tested Bowlby's theory of separation syndrome (the stages of protest, then despair, that Bowlby argued human children demonstrate when separated from their caregivers) by separating infant rhesus monkeys from their mothers (van der Horst et al. 2008).

An extension of Bowlby's theory has been the physiological mechanisms of attachment. This research has its origins in the study of stress responses in rat pups and thus represents a feedback loop between the study of human and animal behavior. Bowlby had already proposed that, in humans, separation from an attachment figure represents a signal of danger. The precise physiological responses of rats separated from their mothers have been meticulously tracked through a series of experiments that would be impossible in human children (Polan and Hofer 2016).

The tools to assess individual differences in attachment have also been extended to the study of nonhuman species. For example, Mary Ainsworth's Strange Situation Procedure has been adapted to assess the owner-dog relationship (Rhen et al. 2013; Topál et al. 1998). Results from

these studies generally support the idea that dogs do form attachment bonds with their owners, which can be assessed along the same dimensions of security and insecurity as the parent-child attachment relationship. The same research has been extended to the study of the cat-owner relationship although there is little evidence of an attachment bond with owners within the feline species (Potter and Mills 2015).

## Conclusion

John Bowlby was a pioneer in the field of human psychology, but his work has long-reaching influences on the study of animal behavior as well. This is fitting given how steeped in ethology and animal research the development and application of attachment theory has been. Nearly 60 years after it was first developed, Bowlby's attachment theory continues to generate new research in both human and nonhuman species. Indeed, the lasting generativity of attachment theory is relatively unique in the field and sets John Bowlby apart as one of the most influential psychologists of the twentieth century.

## Cross-References

- ▶ [Animal-Human Interactions](#)
- ▶ [Attachment](#)
- ▶ [Canine Cognition](#)
- ▶ [Evolutionary Psychology](#)
- ▶ [Family](#)
- ▶ [Feline Cognition](#)
- ▶ [Harry Harlow](#)
- ▶ [Imprinting](#)
- ▶ [Konrad Lorenz](#)
- ▶ [Nurturance](#)
- ▶ [Observational Methods](#)
- ▶ [Parenting](#)

## References

- Ainsworth, M. D. S., Blehar, M. C., Waters, E., & Wall, S. (1978). *Patterns of attachment: A psychological study of the strange situation*. Hillsdale: Erlbaum.
- Bowlby, J. (1982). *Attachment and loss, vol. 1: Attachment* (2nd ed.). New York: Basic Books.
- Bretherton, I. (1992). The origins of attachment theory: John Bowlby and Mary Ainsworth. *Developmental Psychology, 28*, 759–775.
- Polan, H. J., & Hofer, M. A. (2016). Psychobiological origins of infant attachment and its role in development. In J. Cassidy & P. R. Shaver (Eds.), *Handbook of attachment* (3rd ed., pp. 117–132). New York: The Guilford Press.
- Potter, A., & Mills, D. S. (2015). Domestic cats (*Felis silvestris catus*) do not show signs of secure attachment to their owners. *PLoS One, 10*, e0135109. doi:[10.1371/journal.pone.0135109](https://doi.org/10.1371/journal.pone.0135109).
- Rhen, T., McGowan, R. T. S., & Keeling, L. J. (2013). Evaluating the Strange Situation Procedure (SSP) to assess the bond between dogs and humans. *PLoS One, 8*, e56938. doi:[10.1371/journal.pone.0056938](https://doi.org/10.1371/journal.pone.0056938).
- Suomi, S. J. (2016). Attachment in Rhesus monkeys. In J. Cassidy & P. R. Shaver (Eds.), *Handbook of attachment* (3rd ed., pp. 133–154). New York: The Guilford Press.
- Topál, J., Miklósi, A., Csányi, V., & Dóka, A. (1998). Attachment behavior in dogs (*Canis familiaris*): A new application for Ainsworth's (1969) strange situation test. *Journal of Comparative Psychology, 112*, 3219–3229.
- van der Horst, F. C. P., LeRoy, H. A., & van der Veer, R. (2008). "When strangers meet": John Bowlby and Harry Harlow on attachment behavior. *Integrative Psychological and Behavioral Science, 42*, 370–388.
- Van Dijken, S. (1998). *John Bowlby: His early life*. New York: Free Association Books.



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## Randy Thornhill

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### Early Life and Educational Background

Thornhill was born on December 7, 1944 in Decatur, Alabama, USA. He obtained a B.S. in Zoology at Auburn University in 1968, an M.S. in Entomology at Auburn in 1970, and a Ph.D. in Zoology at the University of Michigan in 1974. His 633-page Ph.D. dissertation, *The Evolutionary Ecology of the Mecoptera (Insecta)*, reported on his original research on the behavior and ecology of mecopterous insects and included the first study of female mate choice in an animal under field conditions.

### Professional Career

After receiving his Ph.D., Thornhill was a research entomologist for a year in the Department of Entomology and Nematology of the University of Florida in Gainesville, FL. In 1975, he accepted a faculty position in the Department of Biology at The University of New Mexico, Albuquerque, New Mexico, where, as of 2016, he is still on the faculty. His position in 2016 at the University of New Mexico is Distinguished

Professor Emeritus. Since 1975 until present, he has taught courses in evolutionary biology, ecology, and animal behavior at The University of New Mexico. He has had temporary appointments with numerous universities, including the University of Helsinki, the University of Colorado, the University of Melbourne, Kyoto University, Nagoya University, University of Bielefeld, University of Michigan, and Colorado State University.

Thornhill has authored approximately 200 publications, including four research monographs/books. As of 2016, his publications have been cited about 25,000 times.

Thornhill has received various awards for research contributions, including the Senior Distinguished Scientist Award of the Alexander Von Humboldt Foundation, a Guggenheim Fellowship, a Japan Society for Promotion of Science Fellowship, Fellow of the Animal Behavior Society, and Distinguished Entomologist Award from the Department of Entomology, University of Georgia.

Thornhill has served on editorial boards of several scientific journals. He has served as president elect, president, and past president of the Human Behavior and Evolution Society.

### Research Interests

The evolution of human behavior and psychology is the topic of the majority of Thornhill's

publications, including three of his books—one with Craig Palmer, *A Natural History of Rape: Biological Bases of Sexual Coercion*, one with Steve Gangestad, *The Evolutionary Biology of Human Female Sexuality*, and one with Corey Fincher, *The Parasite-stress Theory of Values and Sociality: Infectious Disease, History and Human Values Worldwide*. Judging from the citation record of his papers and books, his research has contributed to a range of disciplines, including ecology, evolutionary ecology, behavioral ecology, evolutionary biology, entomology, ornithology, and human psychology and behavior. His main interest continues to be sexual selection processes, especially female choice.

## Cross-References

- ▶ [Bilateral Symmetry](#)
- ▶ [Comparative Psychology](#)
- ▶ [Cryptic Mate Choice](#)
- ▶ [Estrous](#)
- ▶ [Evolution](#)
- ▶ [Evolutionary Psychology](#)
- ▶ [Extra-Pair Copulation](#)
- ▶ [Female Choice](#)
- ▶ [Good Genes Hypothesis](#)
- ▶ [Hormones and Behavior](#)
- ▶ [Orgasm](#)
- ▶ [Ornamentation](#)
- ▶ [Sexual Attraction](#)
- ▶ [Sexual Selection](#)

## Selected Publications

### Books

Thornhill, R., & Alcock, J. (1983). *The evolution of insect mating systems*. Cambridge: Harvard University Press.

Thornhill, R., & Fincher, C. L. (2014). *The parasite-stress theory of values and sociality: Infectious disease, history and human values worldwide*. New York: Springer.

Thornhill, R., & Gangestad, S. W. (2008). *The evolutionary biology of human female sexuality*. New York: Oxford University Press.

Thornhill, R., & Palmer, C. T. (2000). *A natural history of rape: Biological bases of sexual coercion*. Cambridge, MA: MIT Press.

### Representative Additional Publications

Alcock, J., & Thornhill, R. (2014). The evolution of insect mating systems. In D. M. Shuker & L. W. Simmons (Eds.), *The evolution of insect mating systems* (pp. 275–278). New York: Oxford University Press.

Gangestad, S. W., Thornhill, R., & Garver-Appar, C. E. (2015). Women's sexual interests across the ovulatory cycle: Function and phylogeny. In D. M. Buss (Ed.), *Handbook of evolutionary psychology* (2nd ed., pp. 403–426). New York: Wiley.

Thornhill, R. (2015). Cryptic female choice: A tale about a boy who loved flies. Forward. In A. V. Peretti & A. Aisenberg (Eds.), *Cryptic female choice in arthropods: Patterns, mechanisms and prospects*. New York: Springer.

Thornhill, R., & Fincher, C. L. (2014b). The parasite-stress theory of sociality, the behavioral immune system, and human social and cognitive uniqueness. *Evolutionary Behavioral Sciences*, 8, 257–264.

Thornhill, R., & Fincher, C. L. (2015). The parasite-stress theory of sociality and the behavioral immune system. In V. Zeigler-Hill, L. Welling, & T. K. Shackelford (Eds.), *Evolutionary perspectives of social psychology* (pp. 419–438). New York: Springer.

Thornhill, R., & Gangestad, S. (2015). The functional design and phylogeny of women's sexuality. In T. K. Shackelford & R. Hansen (Eds.), *The evolution of sexuality* (pp. 149–184). New York: Springer.

**Randy Thornhill** is a faculty member in the Department of Biology at The University of New Mexico in Albuquerque, New Mexico, USA. He is an evolutionary biologist with a primary interest in animal behavior and psychology, including human behavior and psychology.

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## Irene M. Pepperberg, PhD

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### Research Interests

Pepperberg was the first to demonstrate that Grey parrots learn best through social interaction and that their abilities with respect to various concepts (e.g., number, relative size, same/different, inferential reasoning by exclusion) are equivalent to those of nonhuman primates, cetaceans, and ~5–6-year-old children. To teach her parrots referential use of English speech, she departed from the standard operant methods in use at the time and adapted Todt's (1975) two-person "model/rival" training technique, by alternating the roles of the person who modeled what the parrot was to learn with that of the person acting as respondent and using referential rewards – a 1:1 correspondence between the label to be trained and the object presented to the parrot for its use of that label. Via this technique, a Grey parrot, Alex, learned to label more than 50 different objects, seven colors, and seven different shapes ("one-", "two-", "three-", "four-", "five-", "six-", or "eight-corner"). He learned to use English number labels ("one" through "eight") to distinguish

quantities of objects, including collections made up of novel objects, heterogeneous sets of objects, and sets in which objects were placed in random arrays. He could perform addition on small sets and with Arabic numerals. He induced the ordinality of his known numbers from their value and the cardinality of new number labels from their position on the number line. He combined his vocal labels to identify proficiently, request, refuse, categorize, and quantify over 100 different objects, including those that varied somewhat from his training exemplars. He had functional use of "no" and of phrases such as "come here," "want X," and "wanna go Y" (X, Y being appropriate object or location labels). He fully understood the concept of same/different: not merely identity versus nonidentity but that two objects could simultaneously be the same with respect to some attributes and different with respect to others. He and another Grey, Griffin, demonstrated, by vocally stating what they saw, the ability to interpret optical illusions (Müller-Lyer, Kanizsa figures, occluded figures) as do humans. Grey parrots have also used English speech in ways that allowed an examination of other advanced cognitive abilities, such as probabilistic inference. Pepperberg has shown that Grey parrots have executive functioning equivalent to that of young children (e.g., by passing the "marshmallow test").

## Early Life, Educational Background

Dr. Pepperberg was born on April 1, 1949, in Brooklyn, NY, and raised in Laurelton (Queens), NY. An early interest in science was fostered by teachers at Andrew Jackson High School. She received a Bachelor of Science in Chemistry from MIT (1969) and a PhD in Chemical Physics at Harvard from the soon-to-be Nobel Laureate, William N. Lipscomb (1976). During her graduate career, she published several papers on molecular orbital theory and boron hydrides. While at Harvard, she realized that her long-standing interest in animal behavior was stronger than her interest in theoretical chemistry. She began attending seminars and auditing courses on the communicative behavior of animals in nature, avian biology, interspecies communication, and on language acquisition in humans, working up to 80 h per week so as not to neglect her doctoral studies. After completing her doctorate, she switched fields completely.

## Professional Career

Moving with her then-husband, Dr. Pepperberg began her career in 1977 at Purdue University, as a research associate in biology and part-time instructor in psychology. With space borrowed from members of the biology department and the purchase of a Grey parrot, she began conducting experiments on interspecies communication and conceptual behavior in an avian subject. Despite the absence of a faculty appointment, she received the first of many NSF grants in 1979 and later a Harry Frank Guggenheim Foundation Fellowship. In 1984, she became a visiting assistant professor in the Anthropology Department at Northwestern University and a member of their Program on Language and Cognition. She remained at Northwestern until January 1991. At that time, she assumed an associate professorship in the Department of Ecology and Evolutionary Biology at the University of Arizona, receiving tenure in May 1994. She concurrently had a faculty appointment in the Department of Psychology and was an affiliate in the Program in

Neuroscience. While at Arizona, she took a leave of absence (1999–2001) to work at the MIT Media Lab to design human-animal-computer and animal-computer interfaces and to explore the use of her research in building intelligent learning systems. Her visit developed into a research position that ended because of budgetary cutbacks at the Lab. To compensate for breaking her contract, MIT created a short-term research situation to enable her to continue her work; the parrot lab moved to Brandeis University, where she was a research associate professor and later an adjunct associate professor until 2013. After a Radcliffe Fellowship (2004–2005), she was invited to join the Vision Lab at Harvard as an unpaid research associate. She began teaching at Harvard in various capacities soon thereafter. Her research since MIT has been supported by two NSF grants and *The Alex Foundation*, a 501(c)(3) nonprofit of which she is the president. In 2013, she moved the parrot laboratory to Harvard's Department of Psychology.

While at the University of Arizona, Dr. Pepperberg was the recipient of numerous awards for teaching and student mentoring and received a John Simon Guggenheim Fellowship. She was made a fellow of the American Psychological Association, the American Psychological Society (now the Association for Psychological Science), the Animal Behavior Society, and the American Ornithologists' Union, was an alternate for the Cattell Award for Psychology, and was nominated for the Weizmann Woman and Science Award.

While at MIT, Dr. Pepperberg received the 2000 Selby Fellowship from the Australian Academy of Sciences, was made a fellow of the American Association for the Advancement of Science (AAAS), and was nominated for the Grawemeyer Award in Psychology, the L'Oreal Women in Science Award, and the Quest Award from the Animal Behavior Society.

Since arriving at Harvard, she has won the 2005 Frank A. Beach Award, given by Division 6 of the American Psychological Association for best paper in the *Journal of Comparative Psychology*; the Christopher Award for her *New York Times* best-selling book, *Alex & Me*; and the

Christopher Clavius S.J. (Sigma Xi) Award from St. Joseph's University. She was a consultant for ITALK (2007–2012), a program for robotics research. She became a fellow of the Eastern and Midwestern Psychological Associations, was renominated for the L'Oreal and Grawemeyer Awards, and was nominated for the Hebb Award (Division 6, APA) and the Exemplar Award (Animal Behavior Society). She served as associate editor of the *Journal of Comparative Psychology* (2011–2016). She has also received numerous teaching awards.

Dr. Pepperberg has served on the editorial boards of seven different journals, on the National Science Foundation Animal Behavior grant review panel, on the board of directors for the Eastern Psychological Association and *Thinking Animals*, on the Science Advisory Board for the Austrian Science Fund, the review panel for the biannual conference on The Evolution of Language (*Evolang*) five times, the executive council for the American Ornithologists' Union (AOU), and as representative to the Ornithological Council for both the AOU and the Cooper Society. She has chaired the Public Affairs Committee and ran a legislative email alert system for the Animal Behavior Society. She is a foreign affiliate of the British Psychological Society.

Dr. Pepperberg has authored or coauthored over 60 peer-reviewed publications and over 80 book chapters, commentaries, and reviews and has given over 60 keynote or plenary addresses, over 370 invited professional presentations, and almost 80 contributed talks and posters. She also speaks several times each year at non-academic outreach events. She is the author of *The Alex Studies* (Harvard University Press) and *Alex & Me* (HarperCollins), co-edited *Animal Cognition in Nature* (Academic Press), and is an associate editor for the *APA Handbook of Comparative Psychology* (2017). She is a yearly contributor to *The Edge* annual question. With respect to the popular press, her research has been featured in articles in venues as diverse as the *New York Times*, *Die Welt*, *National Geographic*, the *Wall Street Journal*, *Audubon Magazine*, and the *New Yorker*; in television programs such as *Scientific American Frontiers*, *Discovery*, *BBC Nature*, and *Nova Science Now*; and in

various outlets in Europe and Japan. After the parrot Alex died in 2007, his obituary was published worldwide, including in *The Economist*, the *New York Times*, *Der Spiegel*, and *Time* magazine.

## Cross-References

- ▶ [Alex the Parrot](#)
- ▶ [Cardinality](#)

## References

- Balda, R., Pepperberg, I. M., & Kamil, A. C. (eds.) (1998). *Animal cognition in nature*. NY: Academic Press.
- Koepke, A., Gray, S. L., & Pepperberg, I. M. (2015). Delayed gratification: A Grey parrot (*Psittacus erithacus*) will wait for a better reward. *Journal of Comparative Psychology*, *129*, 339–346.
- Pepperberg, I. M. (1987). Acquisition of the same/different concept by an African Grey parrot (*Psittacus erithacus*): Learning with respect to categories of color, shape, and material. *Animal Learning & Behavior*, *15*, 423–432.
- Pepperberg, I. M. (1999). *The Alex studies*. Cambridge, MA: Harvard University Press.
- Pepperberg, I. M. (2007). Grey parrots do not always 'parrot': Phonological awareness and the creation of new labels from existing vocalizations. *Language Sciences*, *29*, 1–13.
- Pepperberg, I. M. (2008). *Alex & me*. NY: HarperCollins.
- Pepperberg, I. M. (2010). Vocal learning in Grey parrots: A brief review of perception, production, and cross-species comparisons. In L. Osterhout, E. Brenowitz, & D. Perkel (Eds.), *Brain & language*, *115*, 81–91, special issue.
- Pepperberg, I. M. (2015). Numerical concepts: Grey parrot capacities. In D. Geary, D. Berch, & K. M. Koepke (Eds.), *Evolutionary origins and early development of basic number processing* (pp. 67–89). London, UK: Elsevier.
- Pepperberg, I. M. (2017). Symbolic communication in nonhumans. In J. Call, I. M. Pepperberg, C. T. Snowdon, & T. R. Zentall (Eds.), *APA handbook of comparative psychology*. Washington, DC: APA Press.
- Pepperberg, I. M., & Brezinsky, M. V. (1991). Relational learning by an African Grey parrot (*Psittacus erithacus*): Discriminations based on relative size. *Journal of Comparative Psychology*, *105*, 286–294.
- Pepperberg, I. M., & Carey, S. (2012). Grey parrot number acquisition: The inference of cardinal value from ordinal position on the numeral list. *Cognition*, *125*, 219–232.

- Pepperberg, I. M., & Hartsfield, L. A. (2014). Do Grey parrots (*Psittacus erithacus*) succeed on a “complex” foraging task failed by primates but solved by fish? *Journal of Comparative Psychology*, *128*, 298–306.
- Pepperberg, I. M., & Nakayama, K. (2016). Robust representation of shape by a Grey parrot (*Psittacus erithacus*). *Cognition*, *153*, 146–160.
- Pepperberg, I. M., & Sherman, D. (2000). Proposed use of two-part interactive modeling as a means to increase functional skills in children with a variety of disabilities. *Teaching and Learning in Medicine*, *12*, 213–220.
- Pepperberg, I. M., & Wilcox, S. E. (2000). Evidence for a form of mutual exclusivity during label acquisition by Grey parrots (*Psittacus erithacus*)? *Journal of Comparative Psychology*, *114*, 219–231.
- Pepperberg, I. M., Koepke, A., Livingston, P., Girard, M., & Hartsfield, L. A. (2013). Reasoning by inference: Further studies on exclusion in Grey parrots (*Psittacus erithacus*). *Journal of Comparative Psychology*, *127*, 272–281.
- Todt, D. (1975). Social learning of vocal patterns and models of their application in Grey parrots. *Zeitschrift für Tierpsychologie*, *39*, 178–188.
- Irene M. Pepperberg**, PhD, is a research associate and lecturer in the Department of Psychology at Harvard. She has served a 6-year term as associate editor for the *Journal of Comparative Psychology* (2011–2016). Her interests are in animal cognition and communication, particularly with respect to Grey parrots. She specializes in training parrots to learn to use English speech to communicate referentially with humans and then using this communication code to examine their cognitive processes.



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## Nicola Clayton

Nicola Clayton  
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### The Biography of Professor Nicola Clayton FRS

Known synonymously as The Bird Lady and The Dancing Professor, Nicky's work focuses on the behaviors and cognitive abilities of birds. Indeed it is her passion for birds that led to the development of her career as a scientist and her work in dance. Currently Nicky is the Professor of Comparative Cognition in the Department of Psychology at the University of Cambridge and a Fellow of Clare College, Cambridge. She is also the first ever scientist in residence at Rambert, Britain's flagship touring dance company, a position she has held since 2011, and cofounder of The Captured Thought, a science-arts collaboration which explores the subjective experience of thinking, together with her tango partner, Clive Wilkins, who is artist in residence in the Department of Psychology at the University of Cambridge.

#### Career History

Nicky spent her youth dancing and bird watching in and around Blackpool, a seaside town in the North of England, before going on to read zoology at Pembroke College, University of Oxford,

from 1981 to 1984. This is where she met Lord John Krebs FRS, who was to become a highly influential figure in her scientific development. When applying to Oxford, she wondered whether to read zoology or PPP (Psychology, Physiology, and Philosophy). The clincher was when John Krebs explained that if she were to choose zoology, she could do research on birds at the Edward Grey Institute for Field Ornithology. Indeed her undergraduate research project investigated the role of memory interference in the food-caching habits of marsh tits – a species of titmouse that loves to live where the elm trees grow and obsessively hide food throughout the autumn and winter months and have long-lasting and highly accurate memories of where they have stashed their scattered stores of food.

For her PhD, Nicky went to St. Andrews University in Scotland to study how zebra finches and Bengalese finches learn their songs, focusing on the cues the birds use to decide which tutor(s) to copy, under the supervision of Professor Peter Slater, completing her PhD in just two and a half years. From there, Nicky went to the University of Bielefeld as a Royal Society postdoctoral fellow and was also awarded an Alexander von Humboldt-Stiftung to work with Professor Klaus Immelmann but sadly he passed away briefly before she arrived. Although she had no official mentor, Professor Joachim Bischof took her under his wing, and she very much felt part of his wonderful academic family. She returned to Oxford to work with John Krebs on what was then called a

Science and Engineering Research Council post-doctoral fellowship, before becoming the Department of Zoology's departmental demonstrator (akin to a temporary university lectureship) at Oxford University and taking up a Junior Research Fellowship at Linacre College coupled with a University Research Fellowship with the Agricultural and Food Research Council.

In 1995, she moved to California to take up an assistant professorship at the University of California Davis and rapidly rose through the ranks in the 5 years she was there – first as associate professor then full professor and Chair of the Animal Behaviour Graduate Group. It was a very special time – for that is when she met Dr. Nathan Emery, not only her key collaborator but also now her husband (since 2001). They share the same birthday (but not the same year), and arguably their most influential paper was published in *Nature* on Nathan's 30th birthday.

In 2000, she returned to the UK to take up a lectureship with tenure in the Department of Psychology at the University of Cambridge. In 2002, she was appointed a Reader, and in 2005, she was appointed to her current post as the Professor of Comparative Cognition. She was elected a Fellow of the Royal Society in 2010.

Her science-arts collaborations began in 2009 when she started to collaborate with Mark Baldwin, world-renowned choreographer and Artistic Director of what was then known as the Rambert Dance Company (formerly Ballet Rambert, and now Rambert), on *Comedy of Change*, a new choreographic work in honor of Charles Darwin's bicentenary and the 150th anniversary of "On The Origin Of The Species." She was appointed scientific advisor to Rambert the same year and the scientist in residence in 2011. One year later, she (together with Clive Wilkins) cofounded *The Captured Thought*, which explores the subjective experience of memory, perception, and consciousness by integrating science and the arts using their skills in tango and the performing arts. They have lectured, performed, and delivered workshops all over the globe – in science and arts venues alike.

## Research Contributions

Nicky's research in learning, memory, and cognition in birds has focused on three behaviors: bird-song, food caching, and food sharing.

Her first series of published endeavors for her PhD and initial postdoc focused on how estrildid grass finches, such as zebra finches and Bengalese finches, learn their songs and what the implications of this song tutor choice (Clayton 1987) was on sexual imprinting and mate choice (Clayton 1989). She then applied this way of thinking about behavioral development in birds to a new behavioral paradigm, food caching, to study how birds that rely on memory to hide food for the future develop these skills in hiding food and the effect this experience has on the development of both memory and the hippocampus (Clayton and Krebs 1994) and how this might not only be relevant to spatial memory but also the ability to episodically recall what happened where and when, an ability that had been previously assumed to be unique to humans (Clayton and Dickinson 1998). This finding led to the idea that these food-caching birds might also remember social aspects of caching, such as who was watching when they cached, and if so, whether they would be able to adjust their caching tactics accordingly to protect their stashes of food from being stolen by other birds that had watched them cache (Dally et al. 2006). The most remarkable finding was that only those birds that had had the opportunity to pilfer (steal) other birds' caches in the past engaged in these cache protection tactics (i.e., naïve birds that had not pilfered before did not do so) and that they only did so if they had been observed by a potential pilferer – they did not do so if they had cached in private (Emery and Clayton 2001). Taken together these series of findings about the extraordinary ability of corvids led to the idea that cognition must have evolved independently and probably convergently in the corvids and apes despite obvious differences in body morphology and the neuroarchitecture of their brains (Emery and Clayton 2004).

Subsequent work established that these birds can also plan ahead, not only for other times (Raby et al. 2007) but also for other minds (Ostojic et al. 2013). It was the latter research

that led to the development of the food sharing paradigm, showing that the jays can infer what their mate will desire in the future (Ostojic et al. 2013).

This work has also led to the development of new paradigms for testing humans that rely much less than conventional studies on verbal report, which have been particularly informative in bridging the gap between human cognitive development and comparative cognition (Clayton 2014) and inspiring new models for thinking about human cognition which have translational aspects – for example, the relationship not only between the hippocampus and memory but also obesity (Cheke et al. 2016; Cheke et al. 2017).

Finally, her science and art collaborations have also resulted in published papers that explore the evolution and manifestation of cognition, through the conduit of dance and with inspiration from the birds (Laland et al. 2015; Clayton and Wilkins 2017). Perhaps that is why Nicky has become known as both The Bird Lady and The Dancing Professor.

## References

- Cheke, L. G., Simons, J. S., & Clayton, N. S. (2016). Higher BMI is associated with episodic memory deficits in young adults. *Quarterly Journal of Experimental Psychology*, *69*, 2305–2316.
- Cheke, L. G., Bonnici, H., Clayton, N. S., & Simons, J. S. (2017). Obesity and insulin resistance are associated with reduced activity in core memory regions of the brain. *Neuropsychologia*, *96*, 137–149.
- Clayton, N. S. (1987). Song tutor choice in zebra finches. *Animal Behaviour*, *35*, 714–722. See also Weary, D., & Krebs, J. R. News and views. *Nature* *329*, 485.
- Clayton, N. S. (1989). Song, sex and sensitive phases in the behavioural development of birds. *Trends in Ecology and Evolution*, *4*, 82–84.
- Clayton, N. S. (2014). EPS mid career award lecture. Ways of thinking: From crows to children and back again. *Quarterly Journal of Experimental Psychology*, *68*, 209–241.
- Clayton, N. S. & Dickinson, A. (1998). Episodic-like memory during cache recovery by scrub jays. *Nature* *395*, 272–278. See Jeffrey, K., & O’Keefe, J. News and views. *Nature* *395*, 215–216.
- Clayton, N. S., & Krebs, J. R. (1994). Hippocampal growth and attrition in birds affected by experience. *Proceedings of the National Academy of Sciences*, *91*, 7410–7414.
- Clayton, N. S., & Wilkins, C. (2017). Memory, mental time travel and the Moustachio quartet. *Royal Society Interface Focus*, *30*, 22–26.
- Dally, J. M., Emery, N. J., & Clayton, N. S. (2006). Food-caching western scrub-jays keep track of who was watching when. *Science*, *312*, 1662–1665.
- Emery, N. J., & Clayton, N. S. (2001). Effects of experience and social context on prospective caching strategies in scrub jays. *Nature*, *414*, 443–446.
- Emery, N. J., & Clayton, N. S. (2004). The mentality of crows. Convergent evolution of intelligence in corvids and apes. *Science*, *306*, 1903–1907.
- Laland, K., Wilkins, C. A. P., & Clayton, N. S. (2015). The evolution of dance. *Current Biology*, *26*, R5–R9.
- Ostojic, L., Shaw, R. C., Cheke, L. G., & Clayton, N. S. (2013). Evidence suggesting that desire-state attribution may govern food sharing in Eurasian jays. *Proceedings of the Natural Academy of Science*, *1101*, 4123–4128.
- Raby, C. R., Alexis, D. M., Dickinson, A. & Clayton, N. S. (2007). Planning for the future by western scrub-jays. *Nature* *445*, 919–921. See also Shettleworth, S. J. News and views. *Nature* *445*, 826–828. And Morell, V. Nicola Clayton profile: Nicky and the jays. *Science* *315*, 1074–1075.

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## Nathan Emery

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Nathan Emery is a comparative psychologist with a strong background in neuroscience. He was one of the first UK students to take a Bachelor's degree in Neuroscience, at the University of Central Lancashire, Preston (1990–1993). In 1994, he worked on his PhD with David Perrett on neurons in the superior temporal sulcus of rhesus monkeys tuned to social signals, such as eye gaze direction and intention movements. After completing his PhD in 1997, he moved to the University of California, Davis, working with David Amaral on the role of the amygdala in primate social behavior. Here he met his future wife and collaborator, Nicky Clayton, and his research interests started to change from the brain to cognition and from primates to birds, specifically corvids. In 2000, Emery and Clayton moved to the University of Cambridge; Emery continued his research on the neurobiology of primate social behavior with Barry Keverne at the famous Sub-Department of Animal Behaviour working on the role of the amygdala and prefrontal cortex in marmoset parental and sexual behavior, but he increasingly devoted more of his time to studies of caching behavior in western scrub jays with Clayton. This latter work resulted in a paper published in

*Nature*, which may be a first in science. The two authors are married and share the same birthday and the paper was published on their joint birthday! In 2002, Emery was awarded a prestigious University Research Fellowship from the Royal Society. This gave him 8 years of funding and freedom to pursue research to support his now celebrated theory that corvids are “feathered apes” because of their similar cognitive abilities with the great apes.

In 2007, Emery moved to Queen Mary University of London to become Senior Lecturer in Cognitive Biology and assist with the development of a new Bachelor's degree in Psychology, as well as establish a research center in psychology with a strong comparative and evolutionary focus. During this time, Emery started a new research program on parrot cognition with his student Jayden van Horik, establishing groups of Hahn's macaws and black-headed caiques. He has also worked with the iconic Tower of London ravens. He has served on the editorial boards of *PLoS ONE*, *Communicative & Integrative Biology*, *Frontiers in Comparative Psychology*, *Journal of Comparative Psychology*, *Current Directions in Behavioural Sciences* and *Animal Cognition*. Recently, he wrote and illustrated a popular science book called *Bird Brain: An Exploration of Avian Intelligence* (Emery 2016) which has now been translated into German, Spanish, Korean and Japanese. A long bout of ill health prevented Emery from taking a more significant role in experimental research, but he continues to play

an active role in the comparative psychology community, especially with respect to public engagement.

Although he started as a neuroscientist and later switched to comparative cognition, he has always maintained an active interest in the brain, especially in how our understanding of neuroscience can inform our understanding of animal minds and vice versa. There are a number of areas to which he has made important contributions:

### **Eye Gaze as a Complex Social Signal**

When Emery started his PhD, Perrett had already found that some neurons in the monkey temporal lobe were selectively responsive to the perception of another's gaze direction; some tuned to gaze looking right, others to gaze looking left, and others to gaze directed at the viewer. However, these neurons were strange because monkeys did not seem capable of using eye gaze as a social cue, for example, to locate hidden food. This was important, because studies of the primate brain were being justified ethically for their utility as a model of the human brain. For example, understanding the system involved in computing where another is looking may be used to model social deficits in individuals with autism. Emery therefore attempted to resolve the issue of why monkeys had failed to respond behaviorally to eye gaze direction cues, when their brains responded automatically to such cues. Through using conspecifics as stimuli, presented as short video clips, as well as recording the subjects' eye movements, he found that monkeys used eye gaze direction to look at objects viewed by another monkey (Emery et al. 1997). He followed this up with a comparative review on gaze processing, breaking it down into subcategories, as well as reviewing the neurobiology of eye gaze. This review has been cited over 1250 times (Emery 2000). Emery continues to work on eye gaze but in birds. He and his PhD student, Auguste von Bayern, found that jackdaws distinguish between different human attentional states when making decisions about when to steal food but only when the human is a

stranger, not a caregiver (von Bayern and Emery 2009). Jackdaws can also use eye gaze and pointing cues to locate hidden food from both humans and conspecifics, but only when the cues are deliberately communicative, such as when moving attention from the viewer to the attended object.

### **Role of the Amygdala in Primate Social Behavior**

Studies by Arthur Kling in the 1960s and 1970s had focused the idea that the amygdala plays an important role in primate social behavior. Amygdala-lesioned monkeys acquired devastating social deficits; losing their dominance status and becoming socially isolated. However, such studies were fraught with interpretational problems, as the lesions were crude, damaging more than the amygdala, including fibers of passage, and the surrounding cortex, hippocampus, etc. A more selective procedure was required to destroy only the amygdala, leaving everything else intact. Ibotenic acid, a selective neurotoxin, fulfilled this role, with MRI-guided lesions to make sure that only the amygdala was damaged. Finally, the behavioral analyses performed by Kling (who was a psychiatrist, not an expert in primate behavior) were rather simplistic. David Amaral therefore assembled a team of neurosurgeons, anatomists, and primatologists to determine the detailed behavioral deficits resulting from precise amygdala lesions. Emery had a detailed knowledge of primate brain anatomy and function, as well as an in-depth knowledge of primate social behavior, and so facilitated communication between the neuroscientists and primatologists on the team. They found that amygdala lesions did not cause the social isolation previously described. Conversely, the amygdalotomized monkeys were more socially attractive, being more approachable, perceived as less threatening, and more likely to elicit affiliative behavior in others (Emery et al. 2001). The lesions appear to have dampened the natural inclination for adult rhesus monkeys to attack strangers. Studies in larger social groups found similar effects, and this

research has continued to focus on social development (albeit without Emery).

## Cache Protection Strategies as Social Cognition

Although the exceptional long-term memories of caching birds had been a popular target of ethological research, very little was known about another threat to successful cache recovery: cache pilfering. Evidence suggested that corvids were different from other caching animals, as they could observe another bird caching, and remember the location of their caches when they came back to them later without the original cacher present, i.e., they had observational spatial memory. Such a skill meant that caching corvids had to implement strategies to minimize cache theft. Following on from Clayton's seminal studies on episodic-like memory in scrub jays, Emery and Clayton found that scrub jays would cache when observed by another bird but attempt to reduce potential cache theft by coming back alone and moving their original caches to new sites (Emery and Clayton 2001). Most intriguingly, this re-caching was only seen in birds that had previous experience of being thieves themselves. The implications for this are that the caching jays may be capable of projecting the specific past experience of pilfering onto another bird with the potential to steal their caches. This is akin to simulation theory of mind, where an individual models another's future actions based on their own experience, using this model to make predictions about what they may be thinking, "putting oneself in another's shoes [when they have worn the same shoes themselves]." In a series of follow-up experiments, Emery, Clayton, and PhD student Joanna Dally found that scrub jays utilized a number of different cache protection strategies, such as caching at a distance, caching behind barriers, and caching in darkened areas. They also appeared aware of who was watching and what they had observed, being more selective in their strategies when specific individuals had spied specific caches being hidden or the individual spy had changed (Dally et al. 2006).

## Convergent Evolution of Cognition

A trickle of studies on corvid cognition over the last 30 years, primarily on complex forms of memory, suggested that corvids were vastly more intelligent birds than had previously been appreciated. Corvid brain size, relative to their body size, was found comparable to that of the great apes, with crows having brains relatively the same size as chimpanzees. Emery and Clayton reviewed evidence from studies of tool-using New Caledonian crows, social cognition in western scrub jays, and long-term memory in pinyon jays and Clark's nutcrackers, amongst others, and concluded that the cognitive abilities of members of the corvid and ape families were strikingly similar. They suggested these similarities had arisen independently in the two groups separated by 300 million years, as thousands of close relatives do not demonstrate the same cognitive skills (Emery and Clayton 2004). It is very likely, but not yet known, whether both families had to face similar socio-ecological problems in their recent evolutionary histories, and whether specific selection pressures, such as trying to locate hidden food distributed across wide swaths of time and space, would have driven the evolution of brains and intelligence capable of overcoming such pressures. Studies on corvid cognition, and direct comparisons with great apes, have blossomed in the years following Emery and Clayton's hypothesis.

## Tasks for Testing Physical Cognition in Non-tool-Using Birds

Emery has been at the forefront of designing cognitive tasks to specifically test physical problem-solving in species that do not use tools. Tool use has been proposed as a specific driver of cognitive evolution, as the ability to use tools is said to require skills in causal reasoning and object manipulation not found in species that do not use tools to procure their food. However, one problem with this assertion was that all tests for physical cognition, such as the classic trap tube task, were designed to only test tool-using



animals, i.e., subjects had to insert a tool into an apparatus in order to procure the treat inside. Emery, Clayton, their PhD student Amanda Seed, and Sabine Tebbich designed a new version of the trap tube task which included a pre-inserted tool, so that the subject only had to decide which side to pull (i.e., the side that would lead to the treat being removed from the tube or the other side that would result in the treat falling into a trap). They also included a number of elegant additional designs, such as a nonfunctional trap and a series of controls to remove the use of simple rules as a winning strategy, such as pull from the side furthest from the trap. They found that rooks, a crow that does not use tools in the wild, rapidly learned to pull the inserted stick from the correct side and did so much faster than tool-using chimpanzees. They transferred immediately to novel designs, with one rook passing all controls (Seed et al. 2006). Emery and his student, Chris Bird, then went on to design a number of other physical cognition tasks that could be used to test non-tool-using species for different aspects of their physical cognition, such as the collapsible platform task (Bird and Emery 2009a), *Aesop's Fable* (or water displacement; Bird and Emery 2009b) task, and the peephole task, measuring looking time in birds. These tasks revealed hitherto unknown abilities in rooks. Bird and Emery (2009a) also found that rooks could make complex tools, such as bending wire into hooks to reach food located in a small bucket at the bottom of a vertical tube (Bird and Emery 2009a). This had only been previously demonstrated in one captive New Caledonian crow, whereas four rooks solved the task on the first trial it was presented, with no natural propensity to make hook (or any) tools.

## Cross-References

- ▶ [Amygdala](#)
- ▶ [Caching](#)
- ▶ [Causal Reasoning](#)

- ▶ [Comparative Cognition](#)
- ▶ [Comparative Psychology](#)
- ▶ [Convergent Evolution](#)
- ▶ [Corvids](#)
- ▶ [Gaze-Following](#)
- ▶ [Nicola Clayton](#)
- ▶ [Psittacine Cognition](#)
- ▶ [Social Cognition](#)
- ▶ [Zoology](#)

## References

- Bird, C. D., & Emery, N. J. (2009a). Insightful problem solving and creative tool modification by captive rooks. *Proceedings of the National Academy of Sciences USA*, *106*, 10370–10375.
- Bird, C. D., & Emery, N. J. (2009b). Rooks use stones to raise the water level to reach a floating worm. *Current Biology*, *19*, 1410–1414.
- Dally, J. M., Emery, N. J., & Clayton, N. S. (2006). Food-caching scrub-jays keep track of who was watching when. *Science*, *312*, 1662–1665.
- Emery, N. J. (2000). The eyes have it: The neuroethology, evolution and function of social gaze. *Neuroscience & Biobehavioral Reviews*, *24*, 581–604.
- Emery, N. J. (2016). *Bird Brain: An exploration of avian intelligence*. Brighton/Princeton: Ivy Press/Princeton University Press.
- Emery, N. J., & Clayton, N. S. (2001). Effects of experience and social context on prospective caching strategies in scrub jays. *Nature*, *414*, 443–446.
- Emery, N. J., & Clayton, N. S. (2004). The mentality of crows: Convergent evolution of intelligence in corvids and apes. *Science*, *306*, 1903–1907.
- Emery, N. J., Lorincz, E. N., Perrett, D. I., Oram, M. W., & Baker, C. I. (1997). Gaze following and joint attention in rhesus monkeys (*Macaca mulatta*). *Journal of Comparative Psychology*, *111*, 286–293.
- Emery, N. J., Capitanio, J. P., Mendoza, S. P., Mason, W. A., Machado, C. J., & Amaral, D. G. (2001). The effects of bilateral lesions of the amygdala on dyadic social interactions in rhesus monkeys (*Macaca mulatta*). *Behavioral Neuroscience*, *15*, 515–544.
- Seed, A. M., Tebbich, S., Emery, N. J., & Clayton, N. S. (2006). Investigating physical cognition in rooks. *Current Biology*, *16*, 697–701.
- von Bayern, A. M. P., & Emery, N. J. (2009). Jackdaws are sensitive to human attentional and communicative gestures in different contexts. *Current Biology*, *19*, 602–606.

# A

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## Anecdote

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## Synonyms

[Ad hoc sampling](#); [Focal sampling](#); [Single subject](#)

Anecdotes are descriptions of events or phenomena, usually in narrative form. These descriptions can be true, false, or exaggerated, and anecdotes may be intended as accurate, humorous, engaging, or recountings of unexpected observations. In understanding human behavior and interaction, anecdotes are commonly used to delineate or illustrate character and motivations. In the study of history, anecdotes are used to illustrate events consistent with accepted understandings or to raise questions about these understandings (Gossman 2003). In western cultures, anecdotes about animals have an ancient lineage, with early Roman authors such as Aelian and Pliny the Elder describing intriguing instances (as well as accepted facts) about animal behavior, many taken from earlier (often Greek) sources. Aelian (2nd–3rd century AD/1958) offers an instance of dolphins escorting a wounded dolphin away from its human captors after scaring them, positing that humans are much less helpful even to their kin (p. 295). Pliny the Elder (1st century AD/1983) describes a hunter who employs tame and

wild ravens to capture game and a raven who, to secure rainwater in an urn, drops stones into it to raise the water level (p. 373). Such anecdotes continue to the present day. The medieval era offered anecdotes of animals' crimes and punishments (Evans 1987); anecdotes about animals were also used as allegories for human behavior. Much of the understanding of actual animals provided in anecdotes relied on the acceptance of ideas presented by master scholars such as Aristotle, as well as folk beliefs. However, some medieval scholars examined Aristotle's ideas critically. For example, Frederick of Hohenstaufen, writing in the thirteenth century, questioned Aristotle's knowledge of falconry:

on many points that he [Aristotle] cites in his book *On Animals* he reports that others have reported so, although he may not have seen it himself, nor had his informers seen it. For firm reliability is not produced by hearsay. (Translated in Beullens 2007, p. 146)

Montaigne (1580/1958), in his *Apology for Raymond Sebond*, provides numerous anecdotes about intelligent actions of animals to quell human self-admiration. He provides an example of a fox deliberating at water's edge, reasoning about the sounds of water it hears beneath an ice to determine whether it will support its weight. Although Descartes (1637/1971, pp. 42–43) later denied that examples like those of Montaigne showed anything comparable to reasoning and offered the explanation that animals' actions were instead comparable to actions of machines,

his view was not generally accepted by scientists or others, who continued to provide anecdotes of animal intelligence (e.g., Guerrini 2007).

Anecdotes became a scientific problem in light of Darwin's (1871/1896) attempts to support his theory of evolution by natural selection by presenting stories of intelligent action by animals, suggesting a common psychology with humans (Knoll 1997 in *AAA* (*AAA* refers to the Mitchell et al. (1997) reference, *Anthropomorphism, anecdotes, and animals*, from which are cited several chapters.)). For example, he describes a dog growling at a windblown parasol as indicating aggression derived from reasoning that the parasol was moved by an unseen agency (Darwin 1871/1896, p. 95). Darwin passed on his project of finding and evaluating evidence of animal intelligence to fellow scientist and friend Romanes (1882), who compiled enormous collections of animal anecdotes intended as evidence of mind or intelligence, as indicated by animals exhibiting choice and consciousness (p. 2). Romanes combed scientific and popular literature for facts about animal intelligence, loosely using three principles to determine what to accept as facts: they must be from an authority, the actions described must be distinctive and plausible in relation to the animal's goal (and not subject to an obvious alternative interpretation), and, if possible, they should be observed more than once in the type of animal described in the anecdote (pp. viii–ix). Adhering to these principles was difficult, and Romanes asked not only scientific colleagues but the general public for anecdotes and observations of animal intelligence (pp. x–xi). Although Romanes' anecdotes continue to delight, they lost their appeal for scientists when Morgan (1894, pp. 288–290) argued against their use by showing that what appeared to be intelligent action can derive from unintelligent trial and error. He describes his own dog Tony as, anecdotally, showing signs of intelligence when he lifts the latch of a gate to let himself out. But Morgan had observed the inception of this apparently intelligent action 3 weeks earlier, and the development to Tony's final action was a slow process not based on an understanding of the latch mechanism. Morgan (1894, p. 291) believed that "what

we need is careful observation in place of anecdotal reporting"; with such careful observation "we shall acquire a better acquaintance with the psychological processes in animals than we could gain by a thousand anecdotes."

Morgan's claims were supported by Thorndike's (1898/1970) observations of the sequence of animals' attempts to escape when placed in a "puzzle box": an animal had to perform a specific act to escape from the box and needed to repeat the act to escape when replaced in the box. Thorndike (1898/1970, p. 24) objected to the use of anecdotes, which "report only such facts as show the animal at his best":

Dogs get lost hundreds of times and no one ever notices it or sends an account of it to a scientific magazine. But let one find its way from Brooklyn to Yonkers and the fact immediately becomes a circulating anecdote. . . . In short, the anecdotes give really the *abnormal* or *supernormal* psychology of animals.

Contrariwise, observations of individual animals could be used to deny complex cognition in an entire species, as when Pfungst (1911/1965) offered evidence that the horse Hans, who apparently understood how to count, solved problems in arithmetic, and read clocks, was not so clever but was instead responding to body movements of his owner when being questioned about his knowledge. "To remedy [the] defects" of anecdotes, Thorndike (1898/1970, p. 24) remarked, "experiment must be substituted for observation and the collection of anecdotes." Thorndike maintained an indifference to infrequent instances of apparent animal intelligence in his own work, as he never discussed data he presented showing that some cats in his puzzle box solved the problem on the first trial. The view that animals were without intelligence, which Thorndike's experiments promoted but did not always support, was strongly denounced by Mills (1899), who offered an imaginative anecdote to argue against Thorndike's view: he remarks that Thorndike "placed cats in boxes only 20x15x12 inches, and then expected them to act naturally. As well enclose a living man in a coffin, lower him, against his will, into the earth, and attempt to deduce normal psychology from his conduct"

(Mills 1899, p. 266). Mills (p. 273) believed that accurate anecdotes were “not valueless” and that “there is no more reason to set aside reliable anecdotes of animals than of men” (1899, p. 262), yet he maintained that “Comparative psychology is advanced rather by systematic observations and experiments than by anecdotes” (p. 273). Washburn (1908, p. 5) delineated the disadvantages of anecdotal evidence for comparative psychology:

1. The observer is not scientifically trained to distinguish what he sees from what he infers.
2. He is not intimately acquainted with the habits of the species to which the animal belongs.
3. He is not acquainted with the past experience of the individual animal concerned.
4. He has a personal affection for the animal concerned and a desire to show its superior intelligence.
5. He has the desire, common to all humanity, to tell a good story.

Washburn examined one of Romanes’ anecdotes (1882, p. 91) which describes ants’ burial of the dead in individual graves following a funeral procession; however, when some of the grave-digging ants attempted to escape, these ants were killed and all deposited in a single grave. “No funeral procession for them!” Washburn (1908, p. 9) remarks. According to Romanes (1882, p. 91), “The observation seems to have been one about which there could scarcely have been a mistake”; according to Washburn (1908, p. 9), “One is inclined to think it just possible that there was.”

Among naturalists (who wrote for popular audiences, not scientists), anecdotes of observation were commonplace (see Lutts 1990). Burroughs and Muir, by writing of specific encounters with animals and the feelings these engendered, sought to bring out sympathy for animals. Seton and Roberts had observed animals in nature and wrote stories based on their knowledge and anecdotes of particular animals from the animals’ perspective. These men often described animals as sharing similar emotional experiences with humans, elaborating the evidence for the

emotions in the animals’ behavior and context. Muir (1897) provided an extended anecdote of his adventures with the dog Stickeen, who followed him into a snowstorm in Alaska in 1879. As they were making their way back to camp amidst hazardous weather conditions, Muir and Stickeen leapt across many gorges, until one seemed too wide for Stickeen. Muir described Stickeen’s anxiety and refusal to follow him over the expanse, until finally the dog made the attempt and succeeded; Stickeen’s joy at his success followed. Seton was a hunter and knowledgeable about animals but also relied on anecdotes he heard to create his stories. Like other naturalists at the turn of the century, Seton believed that anecdotes are valuable and sought evidence from everyday people about animal activities and published their responses. A great deal of the information provided in journals about birds, for example, was from untrained observers (Hayes 1904). Another naturalist, the Reverend William J. Long, wrote numerous books for children based on his own and (mostly) others’ observations of wild animals. Long’s anecdotes employed an anthropomorphic gloss to understand observations of animal behavior that many believed never happened (e.g., a bird making a cast for its leg injury when it put mud on an injury). Consequently, anecdotes came under scrutiny by other naturalists, particularly Burroughs and then US president, naturalist, and hunter Theodore Roosevelt, who called these naturalists “nature fakers” (see Lutts 1990). For these critics, the main problem was not the anecdote per se (as they were avid users of anecdotes) but rather the falsehoods presented. The same issues that Washburn listed a few years later as problems for scientific anecdotes were acknowledged. Concerns about naturalists’ anecdotes appeared in *Science* in 1904. The first letter, by Wheeler (1904), deplored the fact that the public cannot distinguish sound natural history from “drivel in which animals are humanized beyond all recognition,” claimed that Long’s anecdotes indicated advanced knowledge animals could not possibly have, and noted the “lack of value, which serious students attach to anecdotes as evidences of rational endowment in animals” (p. 348). Others criticized Long as

overly imaginative, jumping to conclusions from little evidence, and describing animal behaviors that no one else has observed. The final essay, by Hayes (1904), questioned Wheeler's (1904) analysis of Long's story of woodcock cast making. She claimed that it was Wheeler, not Long, who believed that cast making implies so much knowledge and understanding of theory and asserted that Wheeler implied "that a man who blows on his fingers to warm them or on his tea to cool it has knowledge of the laws of thermodynamic and is ready to discuss entropy or an indicator diagram" (p. 625).

It is the merest commonplace fact that in order to avoid danger, to lessen pain, to save life, to gain pleasure, human beings are constantly performing acts the underlying principles of which they understand scarcely any better than a woodcock understands the principles of surgery. (p. 625)

Thus, the issues in relation to anecdotes are not only whether or not something happened but how it is to be interpreted if it happened. These issues continue to arise inside and outside scientific circles with people who live closely with animals (see Mitchell et al. 1997).

With the advent of behaviorism in American comparative psychology in the 1920s, concerns about anecdotes as too subjective were extended to all observations of animals, such that any descriptions must be as "objective" as possible, not referring to any mental processes of the animal (Watson 1924). Ethologists and Gestalt psychologists in Europe tended to be less concerned about subjective interpretation and overinterpretation and presumed that adequate description of animal activities required understanding their psychological processes (e.g., goals and emotions) as evident in their behavior (Ellis 1938; Köhler 1925; Mackenzie 1977). Researchers studying apes continued to use psychologically tainted ("anthropomorphic") anecdotes to derive their understanding of their subjects; indeed, after denying the usefulness of anecdotes of ape behavior prior to behaviorism, primatologists "discovered" the same behaviors occurring among their apes, seemingly unaware that this was rediscovery (Mitchell 1999). Complex psychological terminology ("disgust," "insight") in relation to individual activities

required not only specification of the animal's behaviors that implicate the psychological description but also reference to prior related activities that substantiate this interpretation (Köhler 1925). In an attempt to assess the usefulness of anecdotal observations, Hebb (1946, p. 88) examined anthropomorphic observations of chimpanzee behaviors indicating friendliness, aggression, and threat to determine that a completely "objective" categorization of chimpanzee behaviors led to "an almost endless series of specific acts in which no order or meaning could be found." By contrast, "anthropomorphic" (i.e., psychological) descriptions of observed behaviors were much more useful as means for keepers and others to know how to interact safely with the chimpanzees.

Throughout much of the twentieth century, a general attitude against anecdotes remained among scientists, which was usually ignored when researchers desired to present anecdotal evidence consistent with current scientific views (usually about apes: e.g., Goodall 1986), but came to the fore when criticizing other researchers' uses of anecdotes to support different views (e.g., see Mitchell 1993, 1999). Denigration (Keijzer 2013) or elevation (Swartz and Evans 1997 in *AAA*) of animal intelligence could be achieved via an anecdote about one animal that came to be viewed as evidence for the entire species. Initial field research in ethology, and especially in primatology, developed from a sometimes anecdotal methodology to more rigorous observational methods. When Altmann (1974) published her article detailing appropriate sampling methods for specific goals, ad libitum sampling (collecting observations of whatever happens) was viewed as useful only to develop further hypotheses and, perhaps, to learn about rare events. Field researchers in primatology began to use focal animal sampling more extensively, in part supported by sociobiological theory cognizing animals as agents, which led them to interact more directly with animals and, consequently, attempt to take on their perspective (Quiatt 1997 in *AAA*). Such were the attitudes when Griffin (1976) published *The question of animal awareness*, which challenged many



accepted interpretations of animal behavior that denied intelligent action. Numerous scientists noted that, but rarely explicated why, anecdotalism was problematic for Griffin's psychological interpretations of animals' activities. Still, although scientists can and should find anecdotes about animals engaging, anecdotal descriptions cannot be used to discern the *psychological* processes that allow for the behavior of apes or other animals (Heyes 1993; Mitchell commentary in Whiten and Byrne 1988, pp. 259–260). When Whiten and Byrne (1988) argued that anecdotes about animals observed by professional primatologists should be accepted as evidence of “tactical deception,” the response from other scientists was mixed, with some accepting anecdotes and others not. Although skepticism was deemed reasonable toward unique anecdotes, Whiten and Byrne (1988) argued that the anecdotes or ad lib observations reported by different observers could be compiled so as to provide multiple records of the same behavior. The term “anecdote” took on new meaning and was now used to refer to a narrative about an observation described by researchers with background and day-to-day knowledge of the nonhuman subjects of the observation (Whiten and Byrne 1988). This methodology only apparently answered many of the earlier criticisms of anecdotes as sources of knowledge about animals' mental processes (Burghardt commentary in Whiten and Byrne 1988, pp. 248–249). It ignored the need (noted by Morgan (1894), e.g., in relation to his dog's latch opening) for understanding the larger developmental context (prior behaviors) from which the behaviors described psychologically in the anecdote derive. (By contrast, many animal-language researchers and developmental psychologists, with their extensive knowledge of individual animals and children, contextualized behaviors developmentally for interpretation – see Miles 1997; Mitchell 1997; both in *AAA*; Piaget 1947/1972.) The belief that researchers' extensive knowledge of animals would derail inaccurate psychological attributions remained unfounded. Whereas several critics remained skeptical that researchers employing anecdotes knew enough to distinguish between more and less complicated psychological explanations for

behavior (Heyes 1993; Kummer et al. 1990; Mitchell commentary in Whiten and Byrne 1988, pp. 259–260; Mitchell 1997 in *AAA*), few field primatologists seemed concerned by the use of anecdotes of deception to infer mental state attribution in primates (see, e.g., commentaries following Whiten and Byrne 1988). But if we ignore the issue of whether or not one can attribute mental states based on anecdotes or observations of nonhuman animals (and there are good reasons to indicate that one cannot: Lurz 2011; contrary to Bates and Byrne 2007), we are left with the fact that observing and naming behavioral patterns within and across species are essential to field studies and have been essential to ethology and comparative psychology from their beginnings (de Waal 1991). As Hobhouse (1901, pp. 89–90) had earlier noted:

In describing the behaviour of an animal, to use terms derived from human consciousness is often the only way of avoiding intolerable prolixity. Properly guarded and corrected by attention to points of difference as well as resemblance, such usage can lead to so little error that, even if we were ultimately to decide that all animals were automata, no change but that of names would be needed in our account. By “feeling” in an animal, then, we shall mean a state essentially similar in causation and function to that which we know as feeling in ourselves. Whether it is similar in other respects, is a question which we do not decide by merely using the term. And so with similar terms.

In our thinking about anecdotes, we seem consistently to rediscover what we already know.

Attempts to formulate a rationale for using anecdotes (observations presented in a narrative) as a source of evidence for an animal's psychology remain problematic. One suggestion is that if an anecdote is deemed plausible in its description and psychological interpretation, it can count as evidence (Byrne 1997; Rollin 1997; both in *AAA*). But there are often multiple possible psychological interpretations of any given event, such that deciding which one is correct purely from observations is impossible (Lurz 2011; Mitchell 1997 in *AAA*). In addition, plausibility depends on what we currently know about an animal, such that using plausibility as a requirement for the acceptance of an anecdote's veracity means that



anecdotes cannot provide new information, however much they may suggest further research topics. Clearly we need to know the function or goal of an animal's action if we are to understand it (Millikan 1997 in *AAA*), and anecdotes may provide novel hypotheses as to animals' goals. Anecdotes are good for illustration of general findings, as in Goodall's (1986) reframing of anecdotes as "word pictures." Summarizing the then recent state of thinking about anecdotes (see also Silverman 1997 in *AAA*), Mitchell (1997 in *AAA*, pp. 426–427) wrote:

Anecdotes by reliable observers can be accepted as believable evidence that specific *behaviors* occurred (this is, that *this* animal did *this* action and *that* animal did *that* action) when these behaviors can be accurately observed under the viewing conditions employed, anthropomorphic terminology can reasonably be used to label or entitle these behaviors, but the interpretation of these behaviors as scientific evidence for mental state attribution demands the same method used to evaluate the accuracy of anthropomorphism: data should be examined using multiple hypotheses varying in the sorts of mental states they propose (if any). As with any science, the accurate interpretation of evidence depends on the hypotheses and perspectives available; and the available evidence may support multiple hypotheses and perspectives. Note, however, that people concerned with ethics toward animals or control of animal behavior, or those just wanting to interact pleasantly with animals, might reasonably use anecdotes and ordinary common sense to fulfill purposes associated with these concerns and desires.

Almost all primate researchers note odd, unexpected, or apparently psychologically complex behaviors in their animal research subjects, perhaps in the hopes of someday understanding them, and sometimes these are reported. But we need to do the same for other species, about whom we are often less willing to construct complex psychological interpretations (Mitchell 1997 in *AAA*). Recent work focuses on whether or not behaviors described in anecdotes can be extended to other species members (e.g., Rutz et al. 2017). Proposed "new" requirements for the collection of anecdotes (Bates and Byrne 2007), where an anecdote is a record of behaviors made by knowledgeable observers soon after their observation, seem to be what researchers have been using all along: the

observer must have experience with the animal, must record behavioral observations as soon as possible (and use this record rather than later reminiscences), and must observe multiple instances of the behavior. As noted earlier, this method assures one of the existence of the behavior but offers no reason to believe that individual behavioral observations themselves, no matter how accurate, can be used to distinguish between complex and simpler psychological processes (Lurz 2011), however suggestive they may be.

## Cross-References

- ▶ [Anthropomorphism](#)
- ▶ [Language Research](#)

## References

- Aelian. (2nd–3rd century AD/1958). *On animals I, Books I–V* (trans: Scholfield, A. F.). London: Harvard University Press.
- Altmann, J. (1974). Observational studies of behavior: Sampling methods. *Behaviour*, 49, 227–265.
- Bates, L., & Byrne, R. W. (2007). Creative or created: Using anecdotes to investigate animal cognition. *Methods*, 42, 12–21.
- Beullens, P. (2007). Like a book written by God's finger: Animals showing the path toward God. In B. Resl (Ed.), *A cultural history of animals in the medieval age* (pp. 127–151). Oxford: Berg.
- Darwin, C. (1871/1896). *The descent of man; and selection in relation to sex*. Princeton: Princeton University Press.
- de Waal, F. (1991). Complementary methods and convergent evidence in the study of primate social cognition. *Behaviour*, 118, 297–320.
- Descartes, R. (1637/1971). Discourse on the method. In *Philosophical writings* (trans: Anscombe, E. & Geach, P. T.). New York: Bobbs-Merrill.
- Ellis, W. D. (1938). *A source book of gestalt psychology*. London: Routledge & Kegan Paul.
- Evans, E. P. (1987). *The criminal prosecution and capital punishment of animals*. London: Faber & Faber.
- Goodall, J. (1986). *The chimpanzees of Gombe: Patterns of behavior*. Cambridge, MA: Harvard University Press.
- Gossman, L. (2003). Anecdotes and history. *History and Theory*, 42, 143–168.
- Griffin, D. R. (1976). *The question of animal awareness: Evolutionary continuity of mental experience*. New York: Rockefeller University Press.

- Guerrini, A. (2007). Natural history, natural philosophy, and animals, 1600–1800. In M. Senior (Ed.), *A cultural history of animals in the age of the enlightenment* (pp. 121–144). Oxford: Berg.
- Hayes, E. (1904). The writings of William J. Long. *Science*, *19*, 623–626.
- Hebb, D. O. (1946). Emotion in man and animal: An analysis of the intuitive processes of recognition. *Psychological Review*, *53*, 88–106.
- Heyes, C. M. (1993). Anecdotes, training, trapping and triangulating: Do animals attribute mental states? *Animal Behaviour*, *46*, 177–188.
- Hobhouse, L. T. (1901). *Mind in evolution*. London: Macmillan.
- Keijzer, F. (2013). The *Sphex* story: How the cognitive sciences kept repeating an old and questionable anecdote. *Philosophical Psychology*, *26*, 502–519.
- Köhler, W. (1925). *The mentality of apes*. New York: Harcourt Brace & Co.
- Kummer, H., Dasser, V., & Hoyningen-Huene, P. (1990). Exploring primate social cognition: Some critical remarks. *Behaviour*, *112*, 84–98.
- Lurz, R. (2011). *Mindreading animals: The debate over what animals know about other minds*. Cambridge: MIT Press.
- Lutts, R. (1990). *The nature fakers: Wildlife, science & sentiment*. Charlottesville: University Press of Virginia.
- Mackenzie, B. (1977). *Behaviourism and the limits of scientific method*. Atlantic Highlands: Humanities Press.
- Mills, T. W. (1899). The nature of animal intelligence and the methods of investigating it. *Psychological Review*, *6*, 262–274.
- Mitchell, R. W. (1993). Recognizing one's self in a mirror? A reply to Gallup and Povinelli, De Lannoy, Anderson, and Byrne. *New Ideas in Psychology*, *11*, 351–377.
- Mitchell, R. W. (1999). Scientific and popular conceptions of the psychology of great apes from the 1790s to the 1970s: Déjà vu all over again. *Primate Report*, *53*, 1–118.
- Mitchell, R. W., Thompson, N. S., & Miles, H. L. (Eds.). (1997). *Anthropomorphism, anecdotes, and animals*. Albany: SUNY Press.
- de Montaigne, M. (1580/1958). Apology for Raymond Sebond. In *The complete essays of Montaigne* (pp. 318–457). Stanford: Stanford University Press.
- Morgan, C. L. (1894). *An introduction to comparative psychology*. London: Walter Scott.
- Muir, J. (1897). An adventure with a dog and a glacier. *Century Magazine*, *54*, 769–776.
- Pfungst, O. (1911/1965). *Clever Hans (The horse of Mr. von Osten)*. New York: Holt, Rinehart & Winston.
- Piaget, J. (1947/1972). *The psychology of intelligence*. Totowa: Littlefield, Adams & Co.
- Pliny. (1st century AD/1983). *Natural history, Books 8–11* (2nd ed., trans: Rackham, H.). London: Harvard University Press.
- Romanes, G. J. (1882). *Animal intelligence*. London: Kegan Paul.
- Rutz, C., Sugasawa, S., van der Wal, J., Klump, B., & St. Clair, J. (2017). Tool bending in New Caledonian crows. *Royal Society Open Science*, *3*(160439), 1–4.
- Thorndike, E. L. (1898/1970). Animal intelligence: An experimental study of the associative processes in animals. In E. L. Thorndike (Ed.), *Animal intelligence: Experimental studies* (pp. 20–155). Darien: Hafner.
- Washburn, M. F. (1908). *The animal mind: A text-book of comparative psychology*. New York: Macmillan.
- Watson, J. B. (1924). *Psychology from the standpoint of a behaviorist* (2nd ed.). Philadelphia: J. B. Lippincott.
- Wheeler, W. M. (1904). Woodcock surgery. *Science*, *19*, 347–350.
- Whiten, A., & Byrne, R. W. (1988). Tactical deception in primates. *Behavioral and Brain Sciences*, *11*, 233–273.

# A

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## Anagenesis

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In the general sense, evolution can be characterized by three distinct phenomena: (1) adaptation, the remarkable fit between an organism and its environment, (2) diversity, the great variety of extinct and extant organisms, and (3) complexity, the intricacy of the organization of internal and external structure and function (Muller and Olsson 2003). *Anagenesis* refers to the idea that there are directional trends in this complexity. In particular, a hierarchy of increasing levels of organization from the simple to the complex characterizes the diversification of species. As Dobzhansky et al. (1977, p. 236) put it in their classic text *Evolution*, anagenesis creates “organisms with novel characters and abilities beyond those of their ancestors.” In evolutionary biology, anagenesis refers to the progressive evolution of a species resulting in linear descent (phyletic divergence); in contrast, cladogenesis refers to speciation by evolutionary splitting of a lineage (branching) to additional species.

The concept of anagenesis has also been used in comparative anatomy, comparative physiology, comparative endocrinology, as well as comparative psychology (Rensch 1959). Rensch identified

several defining features of anagenesis, including: (1) increased complexity (differentiation), (2) centralization of structures and functions, (3) special complexity and centralization of the nervous system, (4) increased plasticity of structures and functions, and (5) increased independence from the environment and increasing command of environmental factors (progression of autonomy). Of course, independence from the environment is a relative concept, as no organism is ever free from its environment. When applied to the comparative study of behavior, anagenesis has typically referred to the progressive evolution of adaptive behavior, learning ability, or cognitive capacity that is often accompanied by the emergence of new psychological capacities (Gottlieb 1984).

The steps or units of anagenesis are typically referred to as “grades” or, in some cases, “levels” (Aronson 1984). A grade or level can be seen as an ascending series of improvements or increases in complexity of any structural or functional unit of analysis within animal groups that may or may not be closely related from a phylogenetic standpoint (Gottlieb 1984). Grades or levels thus address the ranking of behavioral organization (i.e., ability to exhibit various forms of learning, levels of exploratory behavior) relatively independent of strict evolutionary lineages (phylogenetic relationships). As a result, anagenetic analysis has been used most successfully to characterize grades or levels of behavioral complexity at the supraspecific level, that is, across genera, families,

orders, or classes, rather than at the level of species. Examples include patterns of organization of the nervous system, increases in developmental plasticity, and improvements in behavioral versatility or adaptability to environmental change (Yarczower 1998). For example, within the order Chiroptera (bats), researchers have demonstrated that the relatively large brain observed in some bat species is associated with adaptations used to feed on energy-rich foods that are often unpredictable in their spatial distribution (Eisenberg and Wilson 1978). Such descriptions of the specific fit between phenotypes and environments across genera provide a foundation for further studies of both adaptation and diversity.

Schneirla (1949) was among the first comparative psychologists to promote the importance of levels of psychological capacities to frame the comparative study of animal behavior. His anagenetic concept of levels (see Greenberg, this volume) emphasized the value of recognizing and assessing the range of differences in complexity, degree of development, and organization of behavior functions across different types of animal species. This type of approach has been termed “pheneticism” within evolutionary biology (Harvey and Pagel 1991), where grade or level is determined by similarity in phenotypic characters or traits rather than by phylogenetic relationships (common ancestry). For example, Tobach and Schneirla (1968) proposed a hierarchy of behavioral levels based on social and psychological organization: taxis, biotaxis, biosocial, psychotaxis, and psychosocial (see Greenberg, *Behavioral Levels*, this volume). Using this hierarchy, Greenberg (1995) noted that in the general sense, animals demonstrate less behavioral plasticity or versatility function at lower behavioral levels (i.e., taxis, biotaxis), whereas they demonstrate more behavioral plasticity or versatility function at higher behavioral levels at which psychological processes influence the course of behavioral development (i.e., psychotaxis, psychosocial). Importantly, increased behavioral

plasticity is highly correlated with increasing nervous system size, complexity, and organization (Jerison 1973; Jerison and Barlow 1985). Gottlieb (1984) extended this approach to anagenesis by emphasizing that developmental plasticity and behavioral versatility are useful hallmarks of progressive behavioral evolution. He argued that application of this perspective allows a measure of anagenesis to be obtained by comparing different animals’ behavioral adaptability in response to experimentally altered ecological conditions or challenges. However, this ecologically based approach to testing anagenesis has received little research attention to date.

The concept of anagenesis and its use of grades or levels to compare behavioral evolution across animal species independent of strict evolutionary lineages have not been without criticism within comparative psychology (i.e., Capitanio and Leger 1979; Hodos and Campbell 1969, 1990). It is certainly the case that objective criteria for how to best distinguish successive grades or levels of developmental plasticity and behavioral versatility remain poorly defined. Hodos and Campbell (1969, 1990) see comparing evolutionary trends across groups of animals that are not closely related by way of common ancestry as overly subjective and even unscientific. They argue that most comparative psychologists do not base their work on strict evolutionary lineages (i.e., phylogenetic trees), which they view as the appropriate subject matter of a genuine comparative psychology. While such criticisms have been challenged (e.g., Gottlieb 1984; Greenberg 1995), it is clear that an objective description of the criteria used to identify differences in behavioral plasticity or versatility between higher and lower grades of animal species is crucial to the merit and usefulness of anagenetic analysis. Given that the comparative method has been the most general and effective technique for asking questions about the patterns of evolutionary change from Darwin to the present, comparisons of animal behavior and cognition using *both* evolutionary

trends and evolutionary lineages will likely provide a deeper understanding of the phenomena of adaptation, diversity, and complexity.

## References

- Aronson, L. R. (1984). Levels of integration and organization: A reevaluation of the evolutionary scale. In *Behavioral evolution and integrative levels: The TC Schneirla conference series* (pp. 57–81). Hillsdale: Erlbaum.
- Capitanio, J. P., & Leger, D. W. (1979). Evolutionary scales lack utility: A reply to Yarczower and Hazlett. *Psychological Bulletin*, *86*, 876–879.
- Dobzhansky, T., Ayala, F. J., Stebbins, G. L., & Valentine, J. W. (1977). *Evolution*. San Francisco: W.H. Freeman.
- Eisenberg, J. F., & Wilson, D. E. (1978). Relative brain size and feeding strategies in the Chiroptera. *Evolution*, *32*, 740–751.
- Gottlieb, G. (1984). Evolutionary trends and evolutionary origins: Relevance to theory in comparative psychology. *Psychological Review*, *91*, 448–456.
- Greenberg, G. (1995). Anagenetic theory in comparative psychology. *International Journal of Comparative Psychology*, *8*, 31–41.
- Harvey, P. H., & Pagel, M. D. (1991). *The comparative method in evolutionary biology*. Oxford: Oxford University Press.
- Hodos, W., & Campbell, C. B. G. (1969). Scala naturae: Why there is no theory in comparative psychology. *Psychological Review*, *76*, 337–350.
- Hodos, W., & Campbell, C. B. G. (1990). Evolutionary scales and comparative studies of cognition. In R. P. Kesner & D. S. Olson (Eds.), *Neurobiology of comparative cognition* (pp. 1–20). NJ, Erlbaum: Hillsdale.
- Jerison, H. J. (1973). *Evolution of the brain and intelligence*. New York: Academic Press.
- Jerison, H. J., & Barlow, H. B. (1985). Animal intelligence as encephalization. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *308*, 21–35.
- Muller, G., & Olsson, L. (2003). Epigenesis and epigenetics. In B. K. Hall & W. M. Olson (Eds.), *Key words and concepts in evolutionary developmental biology* (pp. 114–123). Cambridge: Harvard University Press.
- Rensch, B. (1959). *Evolution above the species level*. New York: Columbia University Press.
- Schneirla, T. C. (1949). Levels in the psychological capacities of animals. In R. W. Sellars, V. J. McGill, & M. Farber (Eds.), *Philosophy for the future: The quest of modern materialism* (pp. 243–286). New York: McMillan.
- Tobach, E., & Schneirla, T. C. (1968). The biopsychology of social behavior in animals. In R. E. Cooke (Ed.), *The biological basis of pediatric practice* (pp. 68–82). New York: McGraw-Hill.
- Yarczower, M. (1998). Anagenesis. In G. Greenberg & M. M. Haraway (Eds.), *Comparative psychology: A handbook* (pp. 66–70). New York: Garland Publishing.

# D

## Dian Fossey

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### Introduction

Dian Fossey (January 16, 1932, to December 26, 1985) was an American primatologist who dedicated her career to studying and conserving mountain gorillas (*Gorilla beringei ssp. beringei*). In 1967, she established a research site at Karisoke in the Virunga Mountains of Rwanda to study mountain gorillas. Karisoke is currently the longest running field study of wild gorillas and internationally recognized for its scientific outputs and conservation efforts.

### Early Years

During her first trip to Africa in 1963, Fossey visited Olduvai Gorge and met Louis Leakey. Leakey's descriptions of Jane Goodall's pioneering studies of wild chimpanzees at Gombe intrigued Fossey and left a lasting impression. From Olduvai, Fossey traveled to the site where George Schaller had conducted a study of mountain gorillas at Mt. Mikeno in Democratic

Republic Congo (then Zaire). In 1966, Fossey returned to Africa and traveled to Mt. Mikeno with the aim of establishing a research project focused on mountain gorillas. She would eventually identify and habituate several groups of gorillas in the Kabara Region. Fossey was also making progress documenting the behavior of the mountain gorillas when she was evacuated to Uganda due to political unrest in Congo. Not to be deterred from her study of mountain gorillas, Fossey would establish the Karisoke Research Center in the Rwandan portion of the Virunga Mountains in 1967.

### Research Contributions

Fossey obtained her doctoral degree in animal behavior from Cambridge University under the supervision of Dr. Robert Hinde (Fossey 1976) and would make several seminal contributions to understanding gorilla behavior and ecology throughout her academic career. She published many of the first reports of mountain gorilla behavior, including descriptions of their ranging (Fossey 1974), reproduction (Fossey 1982), vocalizations (Fossey 1972), feeding (Fossey and Harcourt 1977), male emigration and female transfer (Harcourt et al. 1976), and ontogeny (Fossey 1979). Many of these publications continue to be relevant and are cited by current publications. Through her popular writings, she was very effective in sharing the rich social lives and



individual personalities of the mountain gorillas with not only the academic community but to a large public audience. Fossey was a visiting associate professor at Cornell University while writing a book entitled “*Gorillas in the Mist*” (Fossey 1983) which remains one of the most widely read books about gorilla behavior. This book provides remarkable insights not only into the daily lives of mountain gorillas but also a riveting first-hand account of the challenging field research conditions and conservation context in which Fossey worked.

## Conservation

Throughout her 20 years studying gorillas in the wild, Fossey was increasingly confronted by the myriad of threats to gorilla survival. The impacts of poaching, the pet trade, and habitat destruction were devastating gorilla populations in the Virunga Mountains and beyond (Harcourt and Fossey 1981). Fossey was outspoken in her conservation efforts, but her “active conservation” tactics were controversial and often aggressive to local people. In December 1977, a male gorilla named “Digit” who Fossey had known for many years was killed by poachers when defending his group. He was speared several times before succumbing to his wounds, which provided time for his family group to flee. This would prompt Fossey to launch the “Digit Fund” to raise funds for conservation and antipoaching efforts in the region. The Digit Fund would later be renamed the Dian Fossey Gorilla Fund International.

## Conclusion

Dian Fossey’s murder shocked the world and the identity of her assailant still remains unknown. Although her personal contributions were cut short by an untimely death, there is no doubt that her research and conservation efforts have had a lasting impact on generations of aspiring scientists and improve the survival prospects of wild apes.

The Karisoke Research Center is internationally renowned for its research and continued vigilance of the dwindling numbers of mountain gorillas in the Virungas. The Dian Fossey Gorilla Fund International has been extremely successful in raising awareness about the plight of wild gorillas and also supports the conservation of many populations of wild gorillas.

## Cross-References

- ▶ [Bushmeat Trade](#)
- ▶ [Field Methodology](#)
- ▶ [Forest](#)
- ▶ [Home Range](#)
- ▶ [Jane Goodall](#)
- ▶ [Observational Methods](#)
- ▶ [Robert Hinde](#)

## References

- Fossey, D. (1972). Vocalizations of the mountain gorilla (*Gorilla beringei*). *Animal Behaviour*, 20, 36–53.
- Fossey, D. (1974). Observations on the home range of one group of mountain gorillas (*Gorilla beringei*). *Animal Behaviour*, 22, 568–581.
- Fossey, D. (1976). The behaviour of the mountain gorilla, Ph.D. dissertation, Cambridge University.
- Fossey, D. (1979). Development of the mountain gorilla (*Gorilla beringei*) through the first thirty-six months. In D. A. Hamburg & E. R. McCown (Eds.), *The Great Apes* (pp. 139–186). Menlo Park: Benjamin-Cummings.
- Fossey, D. (1982). Reproduction among free-living mountain gorillas. *American Journal of Primatology*, 2, 97–104.
- Fossey, D. (1983). *Gorillas in the mist*. Boston: Houghton Mifflin Company.
- Fossey, D., & Harcourt, A. H. (1977). Feeding ecology of free ranging mountain gorilla (*Gorilla beringei*). In T. H. Clutton Brock (Ed.), *Primate ecology: Studies of feeding and ranging behavior in lemurs, monkeys, and apes* (pp. 415–447). London: Academic.
- Harcourt, A. H., & Fossey, D. (1981). The Virunga gorillas – decline of an island population. *African Journal of Ecology*, 19, 83–97.
- Harcourt, A. H., Stewart, K. S., & Fossey, D. (1976). Male emigration and female transfer in wild mountain gorilla. *Nature*, 263, 226–227.

# L

## Learned Helplessness

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The phrase “Learned Helplessness” refers sometimes to a trauma-based empirical phenomenon, sometimes to a cognitive theory about the mechanisms underlying the empirical phenomenon, and sometimes to both at the same time. The empirical phenomenon and the elements of the proposed cognitive mechanism were first introduced by Overmier and Seligman (1967). The basic phenomenon seen in their dogs was a dramatic proactive interference with making and learning coping behaviors, primarily escape behavior, observed a day after having been exposed to 60 unpredictable and uncontrollable 5-sec electric footshocks distributed over an hour. The Learned Helplessness had three features: behavioral, the lack of behavioral coping efforts noted above; associative, a failure to learn the escape response even if they made an escape; and emotional, an apparent passivity to the shocks. Seligman and Maier (1967), in an experiment begun with Overmier (see authors’ footnote), showed that the uncontrollability of the shocks was a critical causal feature for the induction of the Learned Helplessness by using the

so-called “triadic design” paradigm that compared three groups: one group (the Master group) received 60 trials with electric footshocks but was able to escape from or avoid any of the footshocks; a second group (the Yoked group) that was exposed to the same number, duration, and intensity of electric footshocks as experienced by the Master group; and a third group (Normal) that was exposed to the shock apparatus for the same session length but received no shocks. When tested in a second phase 24 h later for their ability to escape in a new apparatus, the Master and Normal groups reliably performed well, while the Yoked group that had experienced the uncontrollable footshocks generally failed to escape at all – they seemed helpless. The degree and duration of this interference is related to the number, duration, and spacing of the trauma experience(s) and can last up to months (Seligman and Groves 1970), and the individual aversive events that make up the trauma cannot be too short (e.g., not less than 1–2 sec) no matter how numerous if one is to produce the Learned Helplessness effect (Overmier and Seligman 1967).

Most are familiar with “Learned Helplessness” which has been cited or invoked in texts more than 3000 times since its introduction and more than 50 times in 2016 according to PsycINFO. Some whole journal issues have been devoted to it. So why has Learned Helplessness remained in the research spotlight? We offer four reasons.

First, the observed phenomenon in the initial experiments was quite dramatic. Induced

“helpless” animals would in phase 2 passively endure a series of minute-long continuous intense footshocks instead of trying to escape. This led to many of follow-up experiments (see review by Overmier and Lolordo 1998) using a number of vertebrate species including humans, fish, mice, and rats and other non-rodent species such as birds and even insects in variety of induction and assessment environments with surprisingly consistent proactive interference results. That is, it was a pretty reliable general phenomenon. Second, “Learned Helplessness” consisted of a syndrome of effects from the first three reported in the initial report of behavioral deficit, a cognitive/learning deficit, and an emotional deficit (anhedonia) to several other less discussed features of the syndrome such as depletions of CNS neurotransmitters (e.g., Anisman et al. 1980), immunosuppression (Laudenslager et al. 1983), enhanced susceptibility to cancer tumor growth (Sklar and Anisman 1979), pain analgesia (Drugan and Maier 1983), anorexia and hypersensitive taste finickiness (Dess et al. 1988), and gastric ulcer (Overmier and Murison 2000). Third, Learned Helplessness became an animal model for testing for antidepressant drugs (e.g., Katz and Sibel 1982). Fourth and most importantly, Seligman (1974) hypothesized that Learned Helplessness in animals closely paralleled reactive depression in humans and that the further study of Learned Helplessness in animals and humans would yield insights into the behavioral, cognitive, and physiological mechanisms of depression. Shortly thereafter, Seligman (1975), in a popular book, extended the application of the presumed cognitive construct underlying Learned Helplessness to a wide variety of other dysphoric psychological phenomena affecting children, adults, and the aged. As Learned Helplessness theory was applied to human dysfunctions, it needed to be enriched with reference to human cognitions and attributions that could be studied (Abramson et al. 1978), but in doing so, it eliminated any *direct* causal chain between specific experiences and the resultant state of Learned Helplessness (see Overmier 1988).

Several reviews of the parallels between Learned Helplessness syndrome and human

depressive psychopathology appeared (e.g., Overmier and Hellhammer 1988), but another by Foa et al. (1992) focused on parallels between Learned Helplessness and post-traumatic stress disorder (PTSD) and argued that Learned Helplessness was better as a model of PTSD. Indeed, some parallels to PTSD do seem more appropriate. A result has been new papers exploring Learned Helplessness as an animal model of PTSD (e.g., Koba et al. 2001). Why didn't Seligman initially link it to PTSD? For starters, PTSD was not a recognized diagnostic entity at the time. Further, of course, PTSD has diagnostic features overlapping with depression. But we note that many of the diagnostic features for PTSD are simply not accessible in animals (e.g., reexperiencing the trauma via flashbacks and reportable nightmares, impaired concentration).

Many of the important proactive effects of Learned Helplessness inducing trauma have been linked to the uncontrollability of the trauma elements. Indeed, as noted, this became part of the definitional nexus for Learned Helplessness. It was certainly what Overmier and Seligman hypothesized in their 1967 paper, and it was what Seligman and Maier tested in their paper.

Mineka and Kihlstrom (1978) argued that dimensions of uncontrollability and unpredictability of events were separate contributory features that induce experimental neuroses. In that line, Overmier and Wielkiewicz (1983) argued that unpredictability of traumatic events is also an important feature for Learned Helplessness induction and has separable – albeit less dramatic – effects from uncontrollability and more specifically that the uncontrollability as one dimension contributed to the behavioral deficit, while unpredictability as an independent dimension contributed to the cognitive/associative/learning deficit of the Learned Helplessness syndrome. Dess et al. (1983) did an interesting confirmatory experiment that showed different temporal loci of effects of unpredictability and uncontrollability on the stressfulness of trauma experiences, both immediate and future ones.

Concurrent with the basic behavioral studies on Learned Helplessness, there was a parallel line of neuroscience analyses of the brain mechanisms

that might underlie Learned Helplessness. Already briefly mentioned above were efforts to find parallels between the behavior and CNS neurotransmitter states and efforts to link findings to psychopharmacological treatments. A promising line of research from the Maier-Watkins laboratory on the neural basis of Learned Helplessness focused much research on the pain perception and the involved neural pathways after experiencing uncontrollable shocks. Special attention was given to the resulting activation of the dorsal raphe nucleus, and this culminated in recent work on the moderating role of the medial prefrontal cortex on the dorsal raphe after experiencing escapable – but not inescapable – shocks (Maier 2015). This new neuroscience work suggests that the *original theory* of Learned Helplessness was wrong in hypothesizing that when events are uncontrollable and unpredictable that organisms learn that their actions are useless and thus they become helpless. Rather, the neuroscience data as reviewed suggest that helplessness is the direct primary result of an activated dorsal raphe and that experiencing controllable and predictable events and learning to control and to predict them are encoded in the medial prefrontal area and suppress the dorsal raphe output. This neuroscience data is exactly congruent with an earlier behavioral hypothesis (Minor et al. 1991) challenging the original Learned Helplessness concept and recharacterizing the nature of the empirical syndrome.

Preventing and overcoming Learned Helplessness is a topic that flows naturally from discovery and elaboration of the syndrome because of its likely important implications for human dysfunction and psychopathology. An understanding of Learned Helplessness should lead investigators to potential new approaches to therapy, prevention, and resilience.

First in this line of investigation, Seligman and Maier (1967) provided evidence that interference of Learned Helplessness was preventable by pretraining the dogs to learn that shock termination was contingent upon responding. Second, Seligman et al. (1968) highlighted the critical role of “taking back control in the face of adversity” by having the dogs guided (forced) to make a

few escape response to terminate shock in the test after being previously exposed to inescapable and uncontrollable traumatic shock. This “putting through therapy” was successful in overcoming the otherwise manifested Learned Helplessness. Third, “therapeutic” action of electroconvulsive shocks was demonstrated in dogs (Dorworth and Overmier 1977) exposed to Learned Helplessness. Fourth, using rats as subjects, cessation conditioning (i.e., signaling the end of inescapable shocks) in the induction phase prevented the development of the interference effect of Learned Helplessness (Minor et al. 1990). Fifth, long-term physical activity prevented one the debilitating neurochemical depletion effects of Learned Helplessness in rats as measured by an attenuation of 5-HT neural activity in the DRN that is thought to play a key role in the expression of Learned Helplessness (Greenwood et al. 2003). Sixth, group housing of mice in an enriched environment wherein the rats had opportunities for play and were spontaneously more active also minimized the negative impact of induced Learned Helplessness in comparison to mice group-housed in an impoverished environment (Chourbaji et al. 2005); the presumed mechanism for this was by supposedly improving physiological moderators of stress such as corticosterone levels among myriad others. Seventh, young rats handled during a 3-week period exhibited fewer negative consequences of Learned Helplessness when tested in adulthood, although no specific mechanism was identified (Costela et al. 1995). This could well be of practical value in child-rearing, although the effects of early handling/maternal separation are complex. Eighth, the efficacy of different pharmacological treatments has been established in many studies and continues to be of great interest (e.g., Takamori et al. 2001). Some of these findings likely have practical value, and all have heuristic value for further researches on Learned Helplessness.

Of course, no line of research is without at least some potential shortcomings. Learned Helplessness has been widely employed as an animal model for understanding mechanisms of depression. However, it is noteworthy that sex differences in animal models of psychopathology may

lead us to question the applicability to men and women. Notably, Dalla et al. (2008) suggested that Learned Helplessness involves sex-specific behavioral effects in rats. The authors observed that the female rats initially exposed to uncontrollable electrical shocks did not show impairment in learning to escape on a subsequent escape task in comparison to male rats that were markedly impaired and did not learn to escape on this novel task. On the other hand, other researchers have found that Learned Helplessness can be induced in both males and females, although estrous state modulates its severity (Jenkins et al. 2001). Although this question of sex differences has not been a major focus of interest so far, it clearly calls for more replications and investigations before drawing any firm conclusions; we believe that it deserves some attention in the future to confirm that Learned Helplessness is a valid animal model of depression, PTSD, and dysphoria relevant for both men and women.

The case of Learned Helplessness is an intriguing one. It emerged from early animal basic science experiments seeking to test aspects of Mowrer's theory of avoidance learning and led to possible applications to humans and therapeutic treatments or immunizations that increase the resilience and coping by humans. It illustrates well how at the outset, one cannot know where basic researches will lead nor their likely future values. In the course of experiments on Learned Helplessness, the field discovered more about behavior, learning, stress, ulcers, pain mechanisms, steroids, opioids, neurotransmitters, and regional processing interactions in the brain and probably about depression, PTSD, and dysphoria. It is still an ongoing story to which new researchers will continue to contribute and more new discoveries will emerge.

## Cross-References

- ▶ [Avoidance](#)
- ▶ [Classical Conditioning](#)
- ▶ [Escape Response](#)
- ▶ [J. Bruce Overmier](#)

## References

- Abramson, L. Y., Seligman, M. E. P., & Teasdale, J. (1978). Learned helplessness in humans: Critique and reformulation. *Journal of Abnormal Psychology, 87*, 49–74.
- Anisman, H., Pizzino, A., & Sklar, L. S. (1980). Coping with stress, norepinephrine depletion and escape performance. *Brain Research, 191*, 583–588.
- Chourbaji, S., Zacher, C., Sanchis-Segura, C., Spanagel, R., & Gass, P. (2005). Social and structural housing conditioning influence the development of a depressive-like phenotype in the learned helplessness paradigm in male mice. *Behavioural Brain Research, 164*, 100–106.
- Costela, C., Tejedor-Real, P., Mico, J. A., & Gibert-Rahola, J. (1995). Effect of neonatal handling on learned helplessness model of depression. *Physiology & Behavior, 57*(2), 407–410.
- Dalla, C., Edgecomb, C., Whetstone, A. S., & Shors, T. J. (2008). Females do not express learned helplessness like males do. *Neuropsychopharmacology, 33*, 1559–1569.
- Dess, N. K., Linwick, D., Patterson, J., Overmier, J. B., & Levine, S. (1983). Immediate and proactive effects of controllability and predictability on plasma cortisol responses to shocks in dogs. *Behavioral Neuroscience, 97*, 1005–1016.
- Dess, N. K., Chapman, C. D., & Minor, T. R. (1988). Inescapable shock increases finickiness about drinking quinine-adulterated water in rats. *Learning and Motivation, 19*, 408–424.
- Dorworth, T. R., & Overmier, J. B. (1977). On “learned helplessness”: the therapeutic effects of electroconvulsive shocks. *Physiological Psychology, 5*(3), 355–358.
- Drugan, R. C., & Maier, S. F. (1983). Analgesic and opioid involvement in the shock-elicited activity and escape deficits produced by inescapable shock. *Learning and Motivation, 14*, 30–47.
- Foa, E., Zinbarg, R., & Rothbaum, B. (1992). Uncontrollability and unpredictability in post-traumatic stress disorder: An animal model. *Psychological Bulletin, 112*, 218–238.
- Greenwood, B. N., Foley, T. E., Day, H. E. W., Campisi, J., Hammack, S. H., Campeay, S., Maier, S. F., & Fleshner, M. (2003). Freewheel running prevents learned helplessness/behavioral depression: Role of dorsal raphe serotonergic neurons. *The Journal of Neuroscience, 23*(7), 2889–2898.
- Jenkins, J. A., Williams, P., Kramer, G. L., Davis, L. L., & Petty, F. (2001). The influence of gender and the estrous cycle on learned helplessness in the rat. *Biological Psychology, 58*, 147–158.
- Katz, R., & Sibel, M. (1982). Animal model of depression: Tests of three structurally and pharmacologically novel antidepressant compounds. *Pharmacology, Biochemistry, and Behavior, 16*, 973–977.
- Koba, T., Kodama, Y., Shimizu, K., Nomura, S., Sugawara, M., Kobayashi, Y., & Ogasawara, T. (2001). Persistent behavioural changes in rats

- following inescapable shock stress: A potential model of post-traumatic stress disorder. *World Journal of Biological Psychiatry*, 2, 34–37.
- Laudenslager, M. L., Ryan, S. M., Drugan, R. C., Hyson, R. L., & Maier, S. F. (1983). Coping and immunosuppression: Inescapable but not escapable shock suppresses lymphocyte proliferation. *Science*, 221, 568–570.
- Maier, S. F. (2015). Behavioral control blunts reactions to contemporaneous and future adverse events: Medial prefrontal cortex plasticity and a cortico-striatal network. *Neurobio Stress*, 1, 12–22.
- Mineka, S., & Kihlstrom, J. F. (1978). Unpredictable and uncontrollable events: A new perspective on experimental neurosis. *Journal of Abnormal Psychology*, 87, 256–271.
- Minor, T. R., Trauner, M. A., Chi-Yuarn, L., & Dess, N. K. (1990). Modeling signal features of escape response: Effects of cessation conditioning in “learned helplessness” paradigm. *Journal of Experimental Psychology: Animal Behavior Processes*, 16, 123–136.
- Minor, T. R., Dess, N. K., & Overmier, J. B. (1991). Inverting the traditional view of “Learned helplessness”: A reinterpretation in terms of anxiety and modulator operations. In M. R. Denny (Ed.), *Fear, avoidance, and phobias: A fundamental analysis* (pp. 87–133). Hillsdale: Erlbaum.
- Overmier, J. B. (1988). Learned Helplessness: State or Stasis of the art. In M. Sabourin, F. Craik, & M. Robert (Eds.), *Advances in psychological science (vol. 2): Biological and cognitive aspects*. Hove: Psychology Press.
- Overmier, J. B., & Hellhammer, D. (1988). The learned helplessness psychological model of human depression. In P. Soubrie, P. Simon, & D. Widlocher (Eds.), *Animal models of psychiatric disorders: vol II. An inquiry into schizophrenia and depression* (pp. 177–202). Basel: Karger.
- Overmier, J. B., & LoLordo, V. M. (1998). Learned helplessness. In W. O’Donohue (Ed.), *Learning and behavior therapy* (pp. 352–373). Boston: Allyn and Bacon.
- Overmier, J. B., & Murison, R. (2000). Anxiety and helplessness in the face of stress predisposes, precipitates, and sustains gastric ulceration. *Behavioural Brain Research*, 110, 161–174.
- Overmier, J.B., & Seligman, M.E.P. (1967). Effects of inescapable shock upon subsequent escape and avoidance responding. *Journal of Comparative and Physiological Psychology*, 63, 28–33. [This is the first paper to describe, characterize, and label “learned helplessness.”]
- Overmier, J. B., & Wielkiewicz, R. M. (1983). On unpredictability as a causal factor in learned helplessness. *Learning and Motivation*, 14, 324–337.
- Seligman, M. E. P. (1974). Depression and learned helplessness. In R. J. Friedman & M. M. Katz (Eds.), *The psychology of depression*. Winston: Washington.
- Seligman, M. E. P. (1975). *Helplessness: On depression, dying, and Death* (pp. 83–125). San Francisco: Freeman.
- Seligman, M. E. P., & Groves, D. (1970). Non-transient learned helplessness. *Psychonomic Science*, 19, 191–192.
- Seligman, M. E. P., & Maier, S. F. (1967). Failure to escape traumatic shock. *Journal of Experimental Psychology*, 74, 1–9.
- Seligman, M. E. P., Maier, S. F., & Geer, J. H. (1968). Alleviation of learned helplessness in the dog. *Journal of Abnormal Psychology*, 73(3), 256–262.
- Sklar, L. S., & Anisman, H. (1979). Stress and coping factors influence tumor growth. *Science*, 205, 513–215.
- Takamori, K., Yoshida, S., & Okuyama, S. (2001). Availability of learned helplessness test as a model of depression compared to a forced swimming test in rats. *Pharmacology*, 63(3), 147–153.



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## Inductive Reasoning

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### Definition

**Inductive reasoning** is a logical process in which multiple premises, all believed true or found true most of the time, are combined to obtain a specific conclusion or to supply evidence for the truth of a conclusion. **Inductive reasoning** is often used to generate predictions or to make forecasts. Inductive reasoning differs from deductive reasoning in that while the conclusion of a deductive inference is certain, the truth of the conclusion of an inductive inference is only probable, where the degree of certainty is based upon the strength (or consistency) of the evidence. In other words, the conclusion of an inductive inference is not a logical certainty (such as when a meteorologist predicts snow). Inductive reasoning also encompasses most cases of where a general principle is derived or where categories are formed based on specific observations (provided that they are probabilistic in nature).

In practice, inductive reasoning is the logical foundation of science, and all fields (from physics to sociology) share the inductive method at their core. (In this regard, it is worth noting that, unlike mathematicians and logicians, scientists can never

be 100% certain about their “truths” and can only make approximations based on accumulated empirical evidence.) But the application of inductive reasoning goes much beyond science and is critical for a multitude of more commonplace and prosaic activities in humans and other animals. Many cognitive activities, ranging from problem solving to social interaction to motor control, can be seen as containing an element of inductive reasoning.

### Introduction

Inductive reasoning is one of the most important and ubiquitous of all problem-solving activities, and its use by nonhuman animals is of great interest within fields of psychology and biology such as cognitive psychology, ethology, evolutionary biology, learning, and neuroscience. In its most elementary form, it seems that most animals exhibit some capacity for inductive reasoning. For instance, sea slugs respond to a stimulus inductively based on past experiences with it (e. g., by “concluding” that the stimulus can be ignored; a case of habituation). Similarly, the fear response of a rodent to a stimulus that was repeatedly and predictably presented in conjunction with a harmful outcome is to some extent the result of an inferential prediction (i.e., the rodent “concludes” by induction that a bright light always precedes a foot shock). And Pavlov’s dogs salivated in response to the ring of a bell

that always came before meal time (the dogs “concluded” by induction that bells are a signal for lunch.)

There exists, however, an old divide on the interpretation of the relevant data on inductive reasoning: Associationism holds that the data can be mostly explained by simple associative processes whereby *reflexes* are modified through experience, while rationalism holds that more complex mechanisms are involved, and the existence of inductive reasoning is required to better explain the data (see Rescorla (1988) for a more complete analysis of these contrasting views).

Traditional associationist models posit that an organism’s learned response to a stimulus is represented by the strength of the relevant associations between stimuli. In this view, the animal adapts to its environment through the process of reflex modification, and that the animal need not make predictions or choose between potential responses. In this sense, reasoning would be unnecessary to explain the examples provided above. Typically, associationists have argued that abstract, rule-governed representations do not really exist and that animals’ (and humans’) behavior can be just as well explained in terms of more specific learned associations between task inputs and outputs. Hence (according to this view), the only thing researchers should be concerned with is the specification of what gets associated with what (easier said than done, but still a relatively straightforward goal). Due in part to the predominance of associationism in psychology during the last century, it was until recently a commonplace assertion that inductive reasoning was beyond the capacity of nonhuman animals. In the past few decades, however, there has been an accumulation of evidence for animal inductive reasoning.

While traditional associationist models assume that an animal’s interaction with the environment is passive (the animal behaves by the automatic adjustment of strengths of association only in reaction to stimuli), rationalist models assume that the interaction is active – the animal actively probes the environment to make determinations about optimizing behavior (Gallistel 2003). In that framework, “figuring things out in nature” is

guided by how useful a stimulus is in reducing the animal’s uncertainty about the time of occurrence of some relevant event. This knowledge comes in part from a distribution of graded degrees of belief over a range of candidate hypotheses, or in other words, it depends on inductive reasoning. Rationalists believe that there are problem-specific computational mechanisms that evolved to inform animals’ behavior (Gallistel 2000). In this light, inductive reasoning is seen as a set of algorithms devoted to particular cognitive processes, such as causal inferences, probabilistic inferences, optimization of strategies from sampling, and categorization/concept formation (Nisbett et al. 1983). Here we will focus on these complex rational solutions that are (mostly) agreed upon to be cases of inductive reasoning.

It should be noted that the higher-order cognition proposed by rationalists and the associative rules proposed by associationists are not necessarily mutually exclusive. De Houwer et al. (2016) propose that associative learning is best thought of as an effect (i.e., the impact of paired events on behavior) rather than a specific mental process (e.g., the formation of associations). In other words, learning and behavior are mediated by higher-order mental processes akin to problem-solving processes such as inductive reasoning. (For more on that topic, see De Houwer et al. 2016).

## Causal and Probabilistic Inferences

Causal inference is the process of reasoning about a causal connection between events based on the co-occurrence of those events. As noted in the Introduction, there are many parallels between instrumental and classical conditioning phenomena in animals on the one hand and contingency assessment and causal judgments by humans on the other (see Shanks (2007) for a recent review). The scientific framework for thinking about causal inference emerged from the associationists’ work on instrumental conditioning. Nevertheless, despite the extensive evidence that bottom-up processes such as instrumental and Pavlovian learning play a fundamental role in the acquisition of causal knowledge, there is also accumulating

evidence for the involvement of top-down processes of causal induction in animals. In this light, the co-occurrence of events is not simply stimuli for an automatic association but in fact evidence for the animal's rational mechanisms to make inferences about the world.

Some interesting examples help illustrate the case that animals have the capacity for complex causal inference. Takagi et al. (2016) used an expectancy violation procedure in cats similar to what is used with human infants to probe their understanding of causal relations and physical laws. The study asked whether cats can use a causal rule to infer the presence of an unseen object on hearing the noise it made inside a container (Takagi et al. 2016). Cats were presented with either an object dropping out of an opaque container or no object dropping out after hearing either a rattling sound (by shaking the container with the object inside) or no sound (by shaking the empty container). The relation between the sound and the object matched with physical laws in half of the trials (congruent condition) and mismatched in the other half (incongruent condition). Inferring the presence of an unseen object from the noise was predicted to result in longer looking time in the incongruent condition (indicating "surprise," i.e., that the cats' expectancy had been violated). In addition, the cats were also able to predict and reach for an object appearance when the container was turned over. These results all suggest that cats have a causal understanding of auditory stimuli, which is indicative of their capacity for inductive reasoning.

In another example, Cheney et al. (1995) examined if baboons can understand cause-effect relations in the context of social interactions by using a playback experiment. Under natural conditions, dominant female baboons grunt repeatedly to subordinate mothers when attempting to interact with those mothers' infants. The subordinate mothers occasionally respond to these grunts by uttering submissive fear barks. So, in their study, Cheney et al. played causally inconsistent scenarios to the baboons in which a lower-ranking female apparently grunted to a higher-ranking female and the higher-ranking female apparently responded with fear barks. As an important

control to rule out simple associative processes, baboons heard a sequence made causally consistent by the inclusion of grunts from a third female that was dominant to both of the others. The researchers found that baboons responded very differently to each scenario: in the causally consistent scenario, they either ignored the calls or looked briefly in the direction of the speaker, while in the causally inconsistent scenario, the baboons stared (seemingly surprised) for a long time. That suggests that baboons recognize by inductive reasoning the factors that cause one individual to give submissive vocalizations to another.

Even rats also seem capable of some degree of causal reasoning. In one study, Blaisdell et al. (2006) concluded rats are able to derive predictions of the outcomes of interventions after passive observational learning of different kinds of causal models. Those outcomes, according to the study, cannot be explained by associationist models but are instead consistent with inductive reasoning models. As a last example, it is important to note that causal reasoning is also critical for the ability to adapt an object for use as a tool, a skill that has been demonstrated by many animals.

The ability to infer causation also depends on the ability to estimate probabilities, as actions (causes) do not always lead to the outcome (expected effects). Animals often face circumstances in which the best choice of action is not certain. Because of this, the ability to reason about probabilities has ecological relevance for many species. Environmental cues may be ambiguous, and choices may be risky (for a review on the theoretical side of decision-making under uncertainty, see Trimmer et al. 2011). The use of inductive reasoning to estimate probabilities requires sampling, and for that an individual must be able to estimate proportions.

Multiple species of animals seem to be able to successfully make judgments on proportions. For example, when foraging, animals go to where more will be available by considering the amount of food in alternative locations and the number of other individuals feeding at these different locations (Rugani et al. 2015). Or in a social context, some primates show inequity aversion; they are

able to judge their own effort and payoff *relative* to another individual's (Brosnan and de Waal 2003).

Probabilistic inference goes one step beyond the ability to compare proportions, because the subject also needs to understand the sampling part of the procedure; that is, they need to make inferences about the probable identity of items drawn from populations, based on the distribution of items in those populations. In fact, a study on capuchin monkeys shows that some individuals could make judgments about proportions but could not reason about probabilities (Tecwyn et al. 2017). Capuchins had to select between hidden single-item samples randomly drawn from two jars. In their first experiment, Tecwyn et al. familiarized subjects with the single-item sampling procedure and determined their baseline performance in this task with two populations of items, where each jar contained only preferred or non-preferred items (100% preferred vs. 100% non-preferred), a task that does not involve any probabilistic judgment. In the other experiments, the researchers investigated the ability of the subjects to make inferences about random samples drawn from mixed pools of items in the two jars. Their results revealed that capuchins' performance suffered when the jars had mixed pools, because it required the individuals to reason probabilistically. Some individuals were still able to infer correctly, but not all did so. As the authors later discuss, this suggests that probabilistic inference might also require other complex mental processes such as inhibitory control and working memory.

Probabilistic inferences are not only restricted to apes. Even mice, for example, possess at least a simpler form of that capability (Berkay et al. 2016) and can adaptively modulate their decisions based on their experienced probability of outcomes. Probabilistic inference also seems to play a critical role in animals' social behavior, including decisions made according to game theory (Crowley 2003).

## Optimization of Strategies from Sampling

The capacity of sampling for probabilistic inference is also related to an inductive inference of integrating information together, such as when an animal navigates home by triangulating spatial cues or develops optimal foraging strategies by combining different food densities in each area. In other words, this inductive reasoning optimizes strategies and decision-making by deriving the "whole" from samples of the component parts.

Wass et al. (2012) studied a form of inductive reasoning for foraging in mice using a Binary Tree Maze, inspired by procedures developed in human decision analysis for identifying the most efficient strategies to reach a goal. The Binary Tree Maze is a decision tree that bifurcates (at decision points) into branches. Each decision point is a potential goal location, and the end of each branch terminates in two "leaves," each of which also contains potential goal locations, providing (in this example) a total of 14 potential goals (although only a random selection of goals were baited on any particular trial). In Wass' study, the mice's task was to navigate the maze so as to inspect every potential goal for a piece of food. While there are many possible search strategies (or paths) to visit every node in a decision tree, the vast majority of these paths would be inefficient due to unnecessary node crossings (in other words, they would involve unnecessary retracing of a path or crosses of a location that had already been explored). What distinguishes the Binary Tree Maze from a standard maze learning task is that no single path is "best"; many routes are equally efficient, and a mouse might perform errorlessly across trials yet not follow the same route on successive trials. The degree to which a mouse could comprehend the structure of the maze from successive experiences in it and implement that information from its current location is a reflection of inductive reasoning. In the study, Wass et al. found that in their initial exposures to the decision tree maze, the mice's pattern

of behavior suggested a disorganized random search. However, within six trials, the patterns of individual animals stabilized and remained stable. At the end of several days of testing, many mice were performing at optimal foraging efficiency, suggesting that the mice quickly came to appreciate the underlying structure of the maze and fix on a strategy for its solution. (However, some mice still performed poorly, which is indicative of wide variability in those mice's inductive reasoning.) Furthermore, Wass et al. (2012) also determined if mice were relying on rote paths through the maze or whether they were engaging in an active search of the maze (a requisite for inductive reasoning). To make this determination, each mouse was allowed to begin its exploration of the maze, and upon making its first entry into a second level branch, the adjacent branch was blocked by lowering a black guillotine door. Had a mouse been following a rote (but nominally efficient) path through the maze, this manipulation would have disrupted the utilization of that rote path. Even after this, mice were still able to perform at a high level of efficiency.

This process of optimization of search is also seen in animals as evolutionarily distant from mammals as honey bees. Naug and Arathi (2007) investigated possible sampling and decision rules that the foragers use to choose one option over another by presenting foragers with choice tests in a foraging arena. They showed that a large part of the sampling and decision-making process of a foraging honey bee can be explained by decomposing the choice behavior into dichotomous decision points and incorporating the cost of sampling. The results suggest that a honey bee forager, by using a few simple rules as part of a probabilistic inference process, is able to effectively deal with the complex task of successfully exploiting foraging patches that consist of dynamic and multiple options (Naug and Arathi 2007).

## Categorization

When encountering a new object in one's surroundings, the ability to recognize the item as a

member of a known category, such as a potential food item or predator, can be crucial for survival. This process involves inductive reasoning given that it requires derivation of general principles from specific, sample observations (extracting the relevant rule out of limited samples and multiple options). Categorization has been well documented empirically, and many animals possess that ability.

In the 1960s, Herrnstein and Loveland (1964) showed that pigeons could learn to peck for reinforcement whenever pictures of people appeared on a screen and not to peck whenever pictures without people were presented. Many similar demonstrations followed, where birds and mammals were trained to categorize diverse classes of natural items, from trees and water to other animal species (examples in D'Amato and Van Sant 1988; Roberts and Mazmanian 1988). In addition to natural categories, animals have also successfully classified objects that would have no evolutionary significance to them, such as "cars" and "chairs" (Bhatt et al. 1988), ruling out the possibility that categorization is only based on innate concepts.

Some interesting examples help illustrate the case that animals are able to form categories from sampling the environment. A study with chimpanzees tested the animals' abilities to categorize photographs of natural objects (Tanaka 2001). Chimpanzees were initially trained to match different color photographs of familiar objects from four possible categories. In training, all the comparison stimuli were from the same category in one condition and from different categories in another condition. For all subjects, training performance was consistently better for the "different category" than for the "same category" trials. In probe trials after training, the sample and positive comparison stimuli were different items from the same category, and the foils were selected from among the three other test categories. Remarkably, individual performance was above chance in probe trials, suggesting that categorization by chimpanzees may transcend perceptual resemblance. Furthermore, the researchers replicated these same results later using novel stimulus items from the same four categories. This study

demonstrates that chimpanzees can group perceptually different exemplars within the same category and suggests that these animals formed conceptual representations of the categories.

In an analogous study, Range et al. (2008) presented dogs with a touch-screen testing procedure, which allowed them to test visual discrimination without the presence of social cueing (social cues from humans are known to be a big confounding factor in cognitive/behavioral studies with dogs, as they coevolved to be very sensitive to our cues). They first trained dogs to differentiate between a set of dog pictures and an equally large set of landscape pictures. All subjects learned to discriminate between the two sets and showed successful transfer to novel pictures. Interestingly, presentation of pictures providing contradictory information (novel dog pictures mounted on familiar landscape pictures) did not disrupt performance, which suggests that the dogs made use of a category-based response rule with classification being coupled to category-relevant features (of the dog) rather than to item-specific features (of the background).

Categorization is not only restricted to visual patterns; of course, it is just that those stimuli are easier for humans to study. In an investigation of categorization of song notes in great tits (Weary 1990), the birds were trained first to discriminate between two synthetic song notes. These sounds were models of naturally occurring song notes and differed from one another in five acoustic parameters. Once the birds learnt to discriminate between the two training notes, they were tested with notes that presented all combinations of the five parameters. Responses to these sounds showed that great tits relied almost exclusively on note frequency to form categories; other parameters such as amplitude modulation, frequency modulation, and the interaction between frequency and amplitude were all used to a much lesser extent.

In light of the abovementioned studies, one might wonder: How is inductive reasoning employed during the formation of categories? There are two main theories on how categorization is formed: exemplar theory and prototype theory. For decades, the exemplar theory was

dominant in the categorization literature, and it assumes that there is one representational/processing system that serves all needs of categorization. According to the theory, organisms store exemplars as separate, individuated memory traces, refer new items to these stored exemplars, and include them in the category if they are similar enough. However, new research has shown that animals have prior expectations of prototypes (or family resemblance or natural kinds) and exclude exceptional cases (such as a weird looking predator exemplar from their list of that predator). In other words, inductive reasoning does not do the work from scratch in forming categories as expected by the exemplar theory. Instead, animals use inductive reasoning (among other processes) to infer coherent family resemblance based on prototypical categories already in place. In a review piece, Smith et al. (2016) argue that, based on converging evidence from multiple species, exemplar processing is insufficient to account for the available data on categorization. They claim that prototype averaging might be less effective and create errors of categorization in lab experiments (since in hypothetical situations, you can always imagine weird exemplars) but that in nature prototyping is good enough for a world with so many similarities within categories (most eagles look like eagles, most fruit trees look like fruit trees, etc.), and so being attuned to prototypes would be more advantageous for faster decisions. Or as Smith et al. (2016) writes: “family-resemblance categories dominate. Animals are adept at what they experience and what they need. Their adeptness is neither a coincidence nor a disability” (p. 273).

## Conclusion

Inductive reasoning is present in many different animals, and the multiple ways in which it is expressed show continuities in nature: to different degrees and levels of competence, animals seem to be able to perform causal inference, probabilistic inference, optimizations of strategies based on observation, categorization, etc. Thus, animals are



crucial behavioral ambassadors to the study of inductive reasoning in humans.

It is also important to keep in mind that although ubiquitous and important, inductive reasoning in practice can be riddled with problems, even in humans. We are far from the perfect, ideal case from which animals should be compared to, as we, in our daily/ecological (out of the armchair) lives, commit many mistakes in categorization and probabilistic inference (as shown by multiple studies that followed the seminal work of Kahneman and Tversky on how people overlook statistical variables such as sample size, correlation, and base rate when they solve inductive reasoning problems (Tversky and Kahneman 1974).

## Cross-References

- ▶ Analogical Reasoning
- ▶ Categorization
- ▶ Causal Reasoning
- ▶ Deductive Reasoning
- ▶ Generalization
- ▶ Intelligence
- ▶ IQ
- ▶ Learning
- ▶ Working Memory

## References

- Berkay, D., Çavdaroğlu, B., & Balcı, F. (2016). Probabilistic numerical discrimination in mice. *Animal Cognition*, *19*(2), 351–365. <http://doi.org/10.1007/s10071-015-0938-1>
- Bhatt, R. S., Wasserman, E. A., Reynolds, W. F., & Knauss, K. S. (1988). Conceptual behavior in pigeons: Categorization of both familiar and novel examples from four classes of natural and artificial stimuli. *Journal of Experimental Psychology: Animal Behavior Processes*, *14*(3), 219–234. <http://doi.org/10.1037/0097-7403.14.3.219>
- Blaisdell, A. P., Sawa, K., Leising, K. J., & Waldmann, M. R. (2006). Causal reasoning in rats. *Science*, *311*(5763), 1020–1022. <http://doi.org/10.1126/science.1121872>
- Brosnan, S. F., & de Waal, F. B. M. (2003). Monkeys reject unequal pay. *Nature*, *425*(6955), 297–299. <http://doi.org/10.1038/nature01963>
- Cheney, D. L., Seyfarth, R. M., & Silk, J. B. (1995). The responses of female baboons (*Papio cynocephalus ursinus*) to anomalous social interactions: Evidence for causal reasoning? *Journal of Comparative Psychology*, *109*(2), 134–141. <http://doi.org/10.1037/0735-7036.109.2.134>
- Crowley, P. H. (2003). Origins of behavioural variability: Categorical and discriminative assessment in serial contests. *Animal Behaviour*, *66*(3), 427–440. <http://doi.org/10.1006/anbe.2003.2259>
- D'Amato, M. R., & Van Sant, P. (1988). The person concept in monkeys (*Cebus apella*). *Journal of Experimental Psychology: Animal Behavior Processes*, *14*(1), 43–55. <http://doi.org/10.1037/0097-7403.14.1.43>
- De Houwer, J., Hughes, S., & Barnes-Holmes, D. (2016). Associative learning as higher order cognition: Learning in human and nonhuman animals from the perspective of propositional theories and relational frame theory. *Journal of Comparative Psychology*, *130*(3), 215–225. <http://doi.org/10.1037/a0039999>
- Gallistel, C. R. (2000). The replacement of general-purpose learning models with adaptively specialized learning modules. In M. S. Gazzaniga (Ed.), *The cognitive neurosciences* (pp. 1179–1191). Cambridge, MA: MIT Press. Retrieved from [http://www.lscnp.net/persons/dupoux/teaching/QUINZAINES\\_RENTREE\\_CogMaster\\_2006-07/Bloc1\\_philo/Preprint\\_replacement\\_of\\_general\\_purpose\\_readiing.pdf](http://www.lscnp.net/persons/dupoux/teaching/QUINZAINES_RENTREE_CogMaster_2006-07/Bloc1_philo/Preprint_replacement_of_general_purpose_readiing.pdf)
- Gallistel, C. R. (2003). Conditioning from an information processing perspective. *Behavioural Processes*, *62* (1–3), 89–101. [http://doi.org/10.1016/S0376-6357\(03\)00019-6](http://doi.org/10.1016/S0376-6357(03)00019-6)
- Herrnstein, R. J., & Loveland, D. H. (1964). Complex visual concept in the pigeon. *Science*, *146*(3643), 549–551. <http://doi.org/10.1126/science.146.3643.549>
- Naug, D., & Arathi, H. S. (2007). Sampling and decision rules used by honey bees in a foraging arena. *Animal Cognition*, *10*(2), 117–124. <http://doi.org/10.1007/s10071-006-0044-5>
- Nisbett, R. E., Krantz, D. H., Jepson, C., & Kunda, Z. (1983). The use of statistical heuristics in everyday inductive reasoning. *Psychological Review*, *90*(4), 339–363. <http://doi.org/10.1037/0033-295X.90.4.339>
- Range, F., Aust, U., Steurer, M., & Huber, L. (2008). Visual categorization of natural stimuli by domestic dogs. *Animal Cognition*, *11*(2), 339–347. <http://doi.org/10.1007/s10071-007-0123-2>
- Rescorla, R. A. (1988). Pavlovian conditioning. It's not what you think it is. *The American Psychologist*, *43*(3), 151–160. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/3364852>
- Roberts, W. A., & Mazmanian, D. S. (1988). Concept learning at different levels of abstraction by pigeons, monkeys, and people. *Journal of Experimental Psychology: Animal Behavior Processes*, *14*(3), 247–260. <http://doi.org/10.1037//0097-7403.14.3.247>
- Rugani, R., Vallortigara, G., & Regolin, L. (2015). The use of proportion by young domestic chicks (*Gallus gallus*). *Animal Cognition*, *18*(3), 605–616. <http://doi.org/10.1007/s10071-014-0829-x>

- Shanks, D. R. (2007). Associationism and cognition: Human contingency learning at 25. *The Quarterly Journal of Experimental Psychology*, *60*(3), 291–309. <http://doi.org/10.1080/17470210601000581>
- Smith, J. D., Zakrzewski, A. C., Johnson, J. M., & Valteau, J. C. (2016). Ecology, fitness, evolution: New perspectives on categorization. *Current Directions in Psychological Science*, *25*(4), 266–274. <http://doi.org/10.1177/0963721416652393>
- Takagi, S., Arahori, M., Chijiwa, H., Tsuzuki, M., Hataji, Y., & Fujita, K. (2016). There's no ball without noise: Cats' prediction of an object from noise. *Animal Cognition*, *19*(5), 1043–1047. <http://doi.org/10.1007/s10071-016-1001-6>
- Tanaka, M. (2001). Discrimination and categorization of photographs of natural objects by chimpanzees (*Pan troglodytes*). *Animal Cognition*, *4*(3–4), 201–211. <http://doi.org/10.1007/s100710100106>
- Tecwyn, E. C., Denison, S., Messer, E. J. E., & Buchsbaum, D. (2017). Intuitive probabilistic inference in capuchin monkeys. *Animal Cognition*, *20*(2), 243–256. <http://doi.org/10.1007/s10071-016-1043-9>
- Trimmer, P. C., Houston, A. I., Marshall, J. A. R., Mendl, M. T., Paul, E. S., & McNamara, J. M. (2011). Decision-making under uncertainty: Biases and Bayesians. *Animal Cognition*, *14*(4), 465–476. <http://doi.org/10.1007/s10071-011-0387-4>
- Tversky, A., & Kahneman, D. (1974). Judgment under uncertainty: Heuristics and biases. *Science*, *185*, 1124–1131. <http://doi.org/10.1126/science.185.4157.1124>
- Wass, C., Denman-Brice, A., Rios, C., Light, K. R., Kolata, S., Smith, A. M., & Matzel, L. D. (2012). Covariation of learning and “reasoning” abilities in mice: Evolutionary conservation of the operations of intelligence. *Journal of Experimental Psychology: Animal Behavior Processes*, *38*(2), 109–124. <http://doi.org/10.1037/a0027355>
- Weary, D. M. (1990). Categorization of song notes in great tits: Which acoustic features are used and why? *Animal Behaviour*, *39*(3), 450–457. [http://doi.org/10.1016/S0003-3472\(05\)80408-7](http://doi.org/10.1016/S0003-3472(05)80408-7)

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# L

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## Laboratory Research

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Knowledge about animals can be gained through research conducted in naturalistic settings as well in captive settings such as zoos, sanctuaries, and laboratories. The type of knowledge that can be gained in these different settings also varies because of the limitations inherent to each setting. For example, observational research conducted in naturalistic settings provides information about the species' behavior in its natural habitat, while similar research in zoos, sanctuaries, and laboratories contributes to our understanding of the core cognitive or learning processes that give rise to the same behavior, although it may be differently manifested in captive settings. Gaining a deeper scientific understanding of a species' behavioral and cognitive abilities including their underlying biological bases, developmental processes, and social influences often requires a controlled environment – an environment that allows for a systematic assessment of different factors on specific behaviors. Such control can be achieved neither in the animals' natural habitats nor in captive settings such as zoos and sanctuaries. Rather, it requires the study of animals, most of which are specifically bred for research in a laboratory

setting, where scientists can control genetic, dietary, social, and other environmental factors that affect behavior and cognition. Methodologies used in laboratory-based studies range from simple observations of animals' behaviors to more complex designs that include manipulating the animal's environment and measuring behavioral outcomes as well as effects on physiological factors such as blood sugar, hormones, and other neurochemicals.

Reliability of research findings depends not only on sound scientific methodology but also on appropriately maintained research animals. A formal system of regulatory oversight of animal research, in the USA, is just over 50 years old. Long prior to the federal system, the research community recognized the value of knowledge that can be gained through laboratory-based animal research and the importance of standards for animal treatment, as is evidenced by the long history of various professional societies addressing the well-being of laboratory animals through the adoption of standards and codes of conduct (see Table 1).

## Federal Oversight

In the USA today, laboratory animal research is a highly regulated activity and involves oversight at multiple levels by different entities. At the federal level, the US Department of Agriculture (USDA) is charged with enforcement of the Animal

**Laboratory Research, Table 1** Historical Developments in Professional and Governmental Attention to Laboratory Animal Wellbeing (Adapted from Dewsbury, D. (*unpublished, personal communication*); Gordon 1999; Schwindaman 1999; Smith et al. 1988)

1904	Director's log at the Hygienic Laboratory, which was the precursor to NIH – <i>Animals are to be used in the proper work of the lab, but anything that inflicts pain upon them will not under any circumstances be allowed</i>
1908	American Medical Association (AMA) issues first set of guidelines for the humane care of animals in laboratory research
1925	<i>APA Committee on Animal Research and Experimentation (CARE)</i> established and APA adopts the <i>AMA Guidelines for Laboratory Animal Care</i>
1949	APA adopts its own set of rules for research with animals, developed by CARE. Most recent revision of the <i>CARE Guidelines</i> was in 2012
1950	NIH Director issues <i>Rules Regarding Animals</i> : Source of animals only from dealers, with stray dogs to be turned over immediately to . . . authorities Comfort and sanitation, with animals on long experiments to be maintained under veterinary supervision Operations to be performed only under the supervision of the director of the institute concerned Anesthesia requirements Treatment of an animal at the close of the experiment, with exception to euthanasia A group of veterinary scientists interested in exchanging information about laboratory animal care establish the Animal Care Panel (ACP), which was the precursor to the American Association for Laboratory Animal Science Institute for Laboratory Animal Resources, ILAR (now called the Institute for Laboratory Animal Research) is established at the National Academies. ILAR is now responsible for the periodic update of <i>The Guide</i>
1963	ACP published the first edition of <i>The Guide</i> . The most recent revision of <i>The Guide</i> was in 2011
1964	ACP tests a pilot program for inspecting and accrediting animal research facilities
1965	American Association for Assessment and Accreditation of Laboratory Animal Care, AAALAC (now called AAALAC International) established
1966	Laboratory Animal Welfare Act (AWA) enacted. It has been amended eight times, with the most recent amendment in 2013
1971	First NIH Policy on Care and Treatment of Laboratory Animals applicable to institutions that receive NIH funding for research with warm-blooded animals
1973	First Public Health Service (PHS) Policy is issued – <i>Principles for Use of Laboratory Animals</i> – it applied to all vertebrate animals
1985	Health Research Extension Act is enacted and provides statutory basis for the PHS Policy AWA amendments pertaining to research passed by Congress – requiring institutions to (1) provide training for all personnel involved in the care and use of animals in research, (2) conduct semiannual inspections of animal research facilities, (3) attend to the psychological well-being of nonhuman primates in research, and (4) provide exercise for research dogs An Interagency Research Animal Committee promulgates the <i>US Government Principles for the Utilization and Care of Vertebrate Animals Used in Testing, Research, and Training</i>
1986	Final version of the <i>PHS Policy on Humane Care and Use of Laboratory Animals</i> went into effect, incorporating provisions mandated by the Health Research Extension Act of 1985

Welfare Act (AWA), which Congress passed in 1966 (Animal Welfare Act of 1966, 2013). The AWA regulates the care and treatment of certain animals that have been bred for sale, for research, or for public exhibition, thus covering animals in a range of settings that include not only dedicated research facilities but also zoos, sanctuaries, entertainment, breeders, and dealers. AWA includes requirements for animal husbandry, handling,

housing, nutrition, sanitation, ventilation, and veterinary care.

Within the USDA, the Animal and Plant Health Inspection Service (APHIS) Animal Care Unit is responsible for the oversight of laboratory animal research. All research facilities that support research with animals covered by the AWA are required to register with APHIS. APHIS fulfills its oversight responsibilities through annual inspections of registered research facilities. The

AWA and ensuing regulations cover research conducted with live or dead dogs, cats, nonhuman primates, guinea pigs, hamsters, rabbits, or other warm-blooded animal except rats of the genus *Rattus*, mice of the genus *Mus*, and birds specifically bred for research.

While research with rats, mice, and birds is not regulated by the USDA under the AWA, the enforcement of standards for the humane care and treatment of these species in research falls within the purview of other federal agencies, including the National Institutes of Health (NIH) Office of Laboratory Animal Welfare (OLAW). OLAW implements the Public Health Service (PHS) Policy on Humane Care and Use of Laboratory Animals (PHS Policy) (Public Health Service Policy on Humane Care and Use of Laboratory Animals 1986). The PHS Policy applies to all live vertebrates used or intended for use in PHS-funded research as well as research funded by the National Science Foundation (NSF).

The Health Research Extension Act of 1985 (Health Research Extension Act 1985) provides the statutory basis for the enforcement of the PHS Policy for PHS-funded research with animals. The PHS Policy requires institutions to use the standards described in *The Guide for the Care and Use of Laboratory Animals (The Guide)* (National Research Council 2011) as the basis for developing and implementing their animal care and use programs. That same year, Congress also amended the AWA to specifically address issues related to improving standards for the humane care and treatment of laboratory animals. In addition, the 1985 AWA amendments included a provision mandating the Secretary of the Department of Agriculture to coordinate with the Secretary of the Department of Health and Human Services on the promulgation of specific requirements under the AWA. Finally, also in 1985, a federal Interagency Research Animal Committee promulgated the US Government Principles for the Utilization and Care of Vertebrate Animals Used in Testing, Research, and Training (US Government Principles) (Office of Science and Technology Policy 1985), which was adopted by all US federal agencies that conduct or support research

with vertebrate animals. The US Government Principles provide a framework for conducting research that complies with both the AWA regulations and the PHS Policy.

OLAW meets its regulatory mandate by requiring institutions that receive PHS funding for research to have an OLAW-approved Animal Welfare Assurance before conducting any research involving vertebrate animals. In the Assurance, the institution attests to compliance with all relevant regulations, the US Government Principles and the PHS Policy. The Assurance also provides detailed information about the institution's animal care and use program, its Institutional Animal Care and Use Committee (IACUC), and an inventory of the species housed at the institution. Similar to the APHIS, OLAW delegates oversight responsibility at the local level to the IACUC, which reviews and approves proposals for research with animals, and submits an annual report to OLAW certifying that semiannual inspections were completed and report serious noncompliance, if any. OLAW evaluates all allegations of noncompliance and conducts approximately ten not-for-cause site visits of assured institutions. The Office also offers education programs focused on sustaining research animal well-being.

## Public Transparency

Federal laws, such the Freedom of Information Act (FOIA) as well as state sunshine laws, provide the general public with access to information regarding research regulated by the USDA and OLAW. Public transparency of the oversight process includes access to USDA and OLAW records, including annual facility reports of the number of animals housed and number involved in research, semiannual inspection reports, and reports of noncompliance, if any.

## Nongovernmental Oversight

In addition to oversight by federal bodies such as APHIS and OLAW, institutions that support

animal research programs can choose to be accredited by a private entity, AAALAC International (formerly known as the Association for Assessment and Accreditation of Laboratory Animal Care International). AAALAC International assesses the institution's animal research program not only to ensure compliance with all relevant federal, state, and local regulations and policies but also the extent to which the animal care and use program meet or exceed the standards set forth in *The Guide*. Institutions that obtain AAALAC International accreditation are required to submit an annual report that provides AAALAC International with up-to-date information on the institution's animal care and use program. AAALAC International conducts site inspections every 3 years to determine whether the institution can maintain its accreditation status. As a private entity, AAALAC is not subject to public records requirements.

### Local Oversight

Both the AWA regulations and PHS Policy assign primary accountability for research animal well-being to the institution through the establishment of an Institutional Animal Care and Use Committee (IACUC). Per the AWA regulations, an IACUC at a USDA-registered facility should consist of, at minimum, three members and include a chairperson, a laboratory animal veterinarian, and a community representative who is unaffiliated with the institution. IACUC functions include a semiannual review of the institutions' program for the humane care and use of animals and a semiannual inspection of the institution's animal facilities. The IACUC is responsible for reporting the findings of its reviews and inspections to the responsible institutional official, noting both minor and significant deficiencies in the program, if any. In the case of significant shortcomings, the IACUC should provide a time line for addressing the identified deficiencies. If the deficiencies are not addressed within the specified time frame, then the IACUC is required to report it to APHIS within 15 days of the lapsed deadline.

The IACUC at an OLAW-assured institution is mandated by PHS Policy to have a minimum of five members – a chairperson, a laboratory animal veterinarian, an affiliated community representative, a scientist with animal research experience, and a nonscientist. The IACUC must submit an annual report to OLAW detailing any changes to the animal care and use program at the institution, the institution's AAALAC accreditation status, IACUC membership, and dates of its semiannual reviews of the institution's animal care and use program and its animal facilities. The IACUC is responsible for promptly reporting to OLAW any serious or continuing noncompliance with the PHS Policy, serious deviations from *The Guide*, and the suspension of any activity by the IACUC. OLAW provides IACUC with detailed guidance on fulfilling its duties.

### IACUC Protocol Review Criteria

In addition to the semiannual reviews and inspections of the institution's animal research program, a major function of the IACUC is to review and approve proposals for the conduct of research studies involving animals. The IACUC is responsible for implementing federal policies as well as state and institutional policies that might be more stringent than federal requirements.

Before approving proposals, the IACUC reviews and documents that the proposed study is not duplicative and that the researcher has considered alternatives to the use of animals for the proposed study. Thus, the protocol must contain a written narrative that describes the research literature as well as the outcome of searches for alternatives on specific databases. The IACUC also ensures that the researcher has described steps that will be taken to minimize any pain and distress, if any, to the animals and how research procedures that involve more than momentary pain and severe or chronic pain or distress will be handled. In addition, the proposal must provide evidence that all research procedures will be conducted by appropriately trained and qualified personnel. The IACUC must ensure that clearly specified requirements for procedures involving



surgery are met and that no animal is used in more than one major operative procedure, unless scientifically justified. The IACUC also must evaluate the appropriateness of species for the proposed study and the number of animals required to obtain scientifically valid results. And lastly, the IACUC ascertains that the animals' living conditions are appropriate. Although assessing the scientific merit (peer review) of proposed research is not within the purview of the IACUC, it is responsible for judging the scientific relevance of the proposed research including its potential to contribute to the health of humans or other animals, to the advancement of knowledge, and/or to the good of the environment or society in general.

In conclusion, laboratory-based research with animals is subject to much more stringent and rigorous oversight than any other activity involving animals, including similar research conducted in other settings such as zoos, sanctuaries, and the wild.

## References

- Animal Welfare Act of 1966, 7 U.S.C. §§ 2131–2156. (2013). Retrieved from [http://www.aphis.usda.gov/animal\\_welfare/downloads/Animal%20Care%20Blue%20Book%20-%202013%20-%20FINAL.pdf](http://www.aphis.usda.gov/animal_welfare/downloads/Animal%20Care%20Blue%20Book%20-%202013%20-%20FINAL.pdf)
- Gordon, H. S. (1999). The history of the public health service policy on the humane care and use of laboratory animals. Retrieved from <https://www.aalas.org/about-aalas/history/50-years-of-lab-animal-science>
- Health Research Extension Act of 1985, Pub. L. No. 99-158, §§ 495, 99 Stat. 820. Retrieved from <https://history.nih.gov/research/downloads/pl99-158.pdf>
- National Research Council. (2011). *Guide for the care and use of laboratory animals* (8th ed.). Washington, DC: National Academies Press. Retrieved from <https://grants.nih.gov/grants/olaw/guide-for-the-care-and-use-of-laboratory-animals.pdf>
- Office of Science and Technology Policy. (1985). United States Government principles for the utilization and care of vertebrate animals used in testing, research, and training. Federal Register, Vol. 50, No 97, 12059. Retrieved from <https://grants.nih.gov/grants/olaw/references/phspol.htm#USGovPrinciples>
- Public Health Service Policy on Humane Care and Use of Laboratory Animals. (1986). Retrieved from <https://grants.nih.gov/grants/olaw/references/phspolicylabanimals.pdf>
- Schwindaman, D. F. (1999). The history of the Animal Welfare Act. Retrieved from <https://www.aalas.org/about-aalas/history/50-years-of-lab-animal-science#.WML7rW8rJpi>
- Smith, S. J., Evans, M., Sullivan-Fowler, M., & Hendee, W. R. (1988). Use of animals in biomedical research: Historical role of the American Medical Association and the American physician. *Archives of Internal Medicine*, 148, 1849–1853.

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# D

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## Dorothy Fragaszy

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Dorothy Munkenbeck Fragaszy grew up on a small farm in a rural part of New York, where the family kept horses, sheep, chickens, and occasionally other livestock. She spent much of her free time riding her horse in the woods and fields and trying to help her father (a mechanical engineer and devoted do-it-yourselfer) to construct and fix things. Her professional interests in animal behavior and problem-solving reflect these early experiences. She earned a BS in Psychology at Duke University (1972) and PhD (1978) in Psychology at the University of California, Davis. Her first research, as a graduate student with W. A. Mason in the 1970s, compared the behavior of captive squirrel monkeys (*Saimiri*) and titi monkeys (*Callicebus*) in novel spaces or facing other unfamiliar challenges. One of the more adventurous studies she conducted involved releasing pairs of monkeys one at a time into a fenced one-acre enclosure, where she had constructed above-ground paths in the center area, and retrieving the pair at the end of an hour by offering them a ride home in their familiar travel-box (Fragaszy 1979). Her studies with squirrel and titi monkeys convinced her that one must interpret a nonhuman

species' behavior in a captive setting in relation to that species' behavior in natural settings. In the case of squirrel and titi monkeys, this meant understanding their distinctly different social systems and foraging ecology, among other things. Titi monkeys form monogamous pairs and live in small territories, traveling together during the day to feed on familiar resources in known locations. In contrast, squirrel monkeys live in large groups, travel in large home ranges, and search for food visually. Monkeys of these two species display different priorities for remaining with a pairmate (titi) versus exploring independently (squirrel monkeys), and remaining in familiar places (titi) versus traveling to new places (squirrel monkeys).

In preparation for studying captive capuchin monkeys, she wanted to learn about these monkeys' lives in a natural setting. Accordingly, she studied foraging behavior and time budgets of weeper capuchins *C. olivaceus* in the llanos of Venezuela as a postdoctoral project (Fragaszy 1990). Subsequently, she established a colony of tufted capuchins in 1982 at San Diego State University, where she held her first faculty position. She took the capuchin monkeys with her to Washington State University in 1984, and finally to the University of Georgia in 1990, where she served as Chair of the Behavioral and Brain Sciences graduate program (and its predecessors) in the Psychology Department from 1995 to 2017, and is currently Professor of Psychology. Her research participants from 1980 to the present are primarily

humans, capuchin monkeys, and chimpanzees, the latter species with the help of collaborators at the Language Research Center of Georgia State University and the Primate Research Institute of Kyoto University. She has collaborated extensively with Elisabetta Visalberghi, with whom she authored, together with Linda Fedigan, *The Complete Capuchin* (a scholarly book about capuchin monkeys).

Dr. Fragaszy's research contributions to the field of animal cognition concern the genesis and expression of behavioral variability and adaptability. The majority of her publications can be grouped into four domains: behavioral development, problem-solving (with an emphasis on spatial problems), motor skills, particularly manual dexterity and skilled actions with objects, and social influences on learning, including traditions. Her studies revealed how young primates (monkeys, apes, humans) explore objects and surfaces using species-typical action routines that adults use to find and extract food and to solve instrumental problems (Fragaszy and Adams-Curtis 1991; Takeshita et al. 2005) and how young monkeys in natural settings become proficient foragers, finding and processing sometimes hidden foods, such as beetle larvae hidden under leaves or inside branches, or snails or shelled fruits that must be cracked open. Her work has sometimes indicated similarities in the actions of nonhuman primates and humans with objects and sometimes revealed striking differences. For example, Dr. Fragaszy has shown that capuchin monkeys and chimpanzees can seriate nesting cups effectively using a motor strategy: placing a cup on another and then removing it if it does not fit into the receiving cup, and repeating the sequence until each cup is contained within the one immediately below (i.e., the set is nested). Her subjects could fit a sixth cup, given after they had seriated a set of five cups, into its position in the middle of the set. This finding calls into question the hypothesis that seriating nesting cups necessarily reflects comprehension that a single cup has dual properties (larger than one, and smaller than another), as this task had been conceptualized in the human developmental literature. Perhaps children, when they first begin to seriate cups, begin with a motor

strategy as well, only later developing comprehension of abstract properties of the component objects (Fragaszy et al. 2002). Similarly, capuchins and chimpanzees align the long axis of a rod or a cross-shaped object to a cutout using a motor/haptic strategy, essentially moving the object across the surface until they feel it drop into the cutout. In this case, however, even two-year-old children can align the long axis of a rod or a cross-shaped object to a cutout, apparently relying on vision to do so (Fragaszy et al. 2015). This finding suggests one reason why monkeys and apes use objects as tools in more limited ways than humans. Nonhuman primates can bring one point of a long object to a point on a surface, as in probing a stick into a hole, but it seems that they cannot precisely align even one axis of one object to an axis in another object, such as the end of a screwdriver with the notch in the head of a screw.

In the domain of manual dexterity, her studies revealed that capuchin monkeys achieve precision grips in diverse forms, occasionally use compound grips (holding two or more objects in one hand using two or more different grips). These are unexpected achievements for New World monkeys because these monkeys' thumbs do not rotate to face the palm, as do the thumbs of Old World monkeys, apes, and humans. While they use precision grips routinely, she has shown that capuchin monkeys do not use in-hand movements (translating or rotating an object wholly with the fingers of one hand) as do chimpanzees, and both species differ considerably from humans in this domain (Craist et al. 2009). Her work on skilled actions with objects also includes studies of tool use, notably by wild capuchin monkeys using stones to hammer open resistant palm nuts. In a series of field experiments conducted with colleagues at the EthoCebus field site in Brazil, she showed that wild monkeys place nuts on an anvil surface in a predictable orientation, so that the more symmetrically curved sides of the nut face the edges of the hemispheric pit in the anvil, and they use exploratory actions before initiating a strike with a hammer stone, strike with accuracy, and control the stone after the strike. These skills apparently depend on haptic perception more than visual perception. They select nuts to crack and

hammer stones with which to crack them taking into account the resistance of the nut to fracture and the composition and mass of the stone (Fragaszy et al. 2010). Kinematic analyses of the striking actions revealed that monkeys modulate features of their movements, such as velocity and amplitude of their striking motions, to accommodate to the demands of the task (whether the nut is starting to crack, for example; Mangalam and Fragaszy 2015) but that they do not control some outcomes of their movements that are characteristic of human skilled percussion (such as regulating the momentum of the stone at impact). Apparently the monkeys can perceive velocity and amplitude of their strikes directly (kinesthetically), as movements of their arms, whereas momentum is a joint function of velocity and the mass of the hammer stone, and cannot be perceived through kinesthesia alone. Taken together, her studies in this area have enriched our understanding of the perceptual foundations of actions with objects, and of the different constraints faced by different species of nonhuman primates in these actions compared to humans. Her work frames the phenomenon of manipulating objects as a problem of movement coordination and management of degrees of freedom of movement, thus linking the phenomenon of using objects as tools to biology, anatomy, and related fields, such as archaeology and robotics.

Finally, Dr. Fragaszy has contributed to our understanding of how nonhuman animals learn with and from others (“socially biased learning”), leading sometimes to the establishment of traditions in the absence of overt teaching or imitation (Fragaszy 2003). She has argued that we need to recognize the power of social coordination of activity in time and space to support young animals’ learning, and that we need to understand the temporal dynamics of social influence and the role of artifacts on learning to advance theory in social learning and cultural evolution (Fragaszy et al. 2013). In this work, capuchin monkeys provide an interesting case. Adult capuchins are highly tolerant of young monkeys remaining near them as they forage and eat, and the adults’ activity strongly influences the young monkeys’ explorations of food and of areas where adults eat

(including where they crack nuts with stones and anvils). Their social dynamics and activity, and the artifacts that the adults produce, support young monkeys’ frequent practice of diverse foraging skills, including using stones and anvils to crack nuts. Practice of relevant actions hones specific motor skills, and it also likely strengthens attentional and memory processes related to these activities. Thus adults scaffold young monkeys’ skilled activity in direct and indirect ways.

Throughout her career, Dr. Fragaszy has consistently sought explanations of behavior in accord with species’ perceptual biases, motor propensities, social proclivities, and motivation to coordinate behavior with others in time and space. Her thinking draws on concepts and methods from developmental psychology, movement science, embodied cognition, niche construction theory, ecological psychology, and dynamical systems theory, as well as ethology. She has pioneered, often together with Elisabetta Visalberghi, new methods of collecting behavioral data in natural and captive settings.

Dr. Fragaszy maintains national and international research collaborations, most notably codirecting the *EthoCebus* project in northern Brazil since 2005 with Patrícia Izar (University of São Paulo), and Elisabetta Visalberghi (National Research Council, Italy). Her international outlook is evident in her long service to the International Primatological Society in which she held several elected offices, including Secretary General and President, between 1989 and 2004. Subsequently she served as President of the American Society of Primatologists, and as Editor of the *Journal of Comparative Psychology*. She has served as doctoral advisor to about two dozen PhDs, mentored several postdoctoral scholars and hundreds of undergraduate research assistants, and hosted many visiting international students and researchers.

## Cross-References

- ▶ [Activity Budget](#)
- ▶ [Affordance Learning](#)
- ▶ [Behavioral Flexibility](#)

- ▶ Cognition
- ▶ Comparative Cognition
- ▶ Development of Behavior
- ▶ Elisabetta Visalberghi
- ▶ Embodied Cognition
- ▶ Goal-directed Behavior
- ▶ Hominoidea Cognition
- ▶ Language Research Center
- ▶ Learning
- ▶ Movement/locomotion
- ▶ Nut-Cracking
- ▶ Perception-Action Theory
- ▶ Planning
- ▶ Platyrrhine Cognition
- ▶ Primate Cognition
- ▶ Primates
- ▶ Problem-solving
- ▶ Social Learning
- ▶ Stone Tools
- ▶ Tool Use

## References

- Craut, J., Fragaszy, D., Hayashi, M. & Matsuzawa, T. 2009. Dynamic in-hand movements in adult and young juvenile chimpanzees (*Pan troglodytes*). *American Journal of Physical Anthropology*, 138 (3), 274-285.
- Fragaszy, D. M. (1979). Squirrel and titi monkeys in a novel environment. In J. Erwin, T. Maple, & G. Mitchell (Eds.), *Captivity and behavior* (pp. 172–216). New York: Van Nostrand.
- Fragaszy, D. M. (1990). Sex and age differences in the organization of behaviour in wedge-capped capuchin monkeys (*Cebus olivaceus*). *Behavioural Ecology*, 1, 81–94.
- Fragaszy, D. M. (2003). Making space for traditions. *Evolutionary Anthropology*, 12, 61–70.
- Fragaszy, D. M., & Adams-Curtis, L. E. (1991). Generative aspects of manipulation in tufted capuchin monkey (*Cebus apella*). *Journal of Comparative Psychology*, 105, 387–397.
- Fragaszy, D., Galloway, A., Johnson-Pynn, J., Hirsh, E., & Brakke, K. (2002). The sources of skill in seriating cups in children, monkeys, and apes. *Developmental Science*, 5, 118–131.
- Fragaszy, D., Greenberg, R., Visalberghi, E., Ottoni, E. B., Izar, P., & Liu, Q. (2010). How wild bearded capuchin monkeys select stones and nuts to minimize the number of strikes per nut cracked. *Animal Behaviour*, 80(2), 205–214.
- Fragaszy, D., Biro, D., Eshchar, Y., Humle, T., Izar, P., Resende, B., & Visalberghi, E. (2013). The fourth dimension of tool use: Temporally enduring artifacts aid primates learning to use tools. *Philosophical Transactions of the Royal Society B*, 368, 20120410.
- Fragaszy, D. M., Kuroshima, H., & Stone, B. W. (2015). “Vision for action” in young children aligning multi-featured objects. *PlosOne*, 10(10), e0140033. doi:10.1371/journal.pone.014033.
- Mangalam, M., & Fragaszy, D. M. (2015). Wild bearded capuchin monkeys crack nuts dexterously. *Current Biology*, 25(10), 1334–1339.
- Takeshita, H., Fragaszy, D., Mizuno, Y., Matsuzawa, T., Tomonaga, M., & Tanaka, M. (2005). Exploring by doing. How young chimpanzees discover surfaces through action with objects. *Infant Behavior & Development*, 28, 316–328.

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## Impossible Task Paradigm

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### Synonyms

[Unsolvable task paradigm](#)

### Definition

Experimental procedure eliciting an immediate and unanticipated *expectancy violation*.

### Introduction

Research in comparative cognition and ethology has grown exponentially in the last few decades, and with this growth, we have seen a diversity of paradigms for studying the cognitive abilities of animals. The impossible task paradigm is one of these developments, and its use provides insight into the decision-making processes of animals, particularly in the realm of expectancy violation.

### Methods and aims of the impossible task paradigm

The impossible task paradigm consists of a number of solvable trials in which the experimental subject solves an easy task to obtain a reward (e.g., food or toy) by manipulating an apparatus, followed by an unsolvable trial in which the reward becomes unreachable. This paradigm is a useful tool for assessing capacities for requesting help and the decision-making process in different species. In fact, it is a widely used procedure used by behavioral scientists who study canine cognition, and particularly how canines communicate with humans while attempting to solve problems.

The impossible task resembles the problem-solving paradigm. However, in the latter the animal tries to solve a task not knowing if it is solvable or not, whereas in the impossible task, the experimental subject initially learns that the task is easy to solve, but afterward the same task becomes unsolvable. The problem-solving task could also become impossible when the animal is not able to solve the task, but the focal element (i.e., violation of expectation) is missing.

The impossible task paradigm can be applied using different devices. Miklósi et al. (2003) used bin-opening and rope-pulling tests in which animals learn to obtain food by opening a bin or pulling on a rope from a cage during training trials. Afterward the animals are exposed to the impossible trial, in which the bin was closed mechanically or a hidden end of the rope was



fastened to the cage, making the task unsolvable. A different device was employed by Marshall-Pescini et al. (2009): for the solvable trials, the apparatus comprised a wooden platform upon which food was placed and covered with an upside down plastic container that could be either moved off the platform or overturned to obtain the food. During the unsolvable trial, the container was screwed to the wooden platform and food became inaccessible. Horn et al. (2012) constructed an impossible task with an apparatus consisting of two wooden discs attached in two-tiered fashion. The lower disc held six round food containers that could be accessed by rotating the upper disk to align it with a hole that allowed the subject to retrieve the food. The apparatus also included a locking mechanism that, when activated, prevented rotation of the upper disc. In Persson et al. (2015), the apparatus consisted of three plates on a solid foundation covered by three transparent lids. The subjects could reach the food inside the plate by sliding a lid to the side. In their experimental setup, one of the three lids was secured, making it impossible to open. In all cited studies, at least one person is present during the test phase (an experimenter or a person who is familiar to the animal), whom remains inactive, leaving the subject free to choose whether to interact with him or her.

Research using the impossible task paradigm with canids focuses on various behaviors that indicate expectancy violation. Generally the most commonly observed behaviors during the unsolvable phase of the tests could be grouped into two broad categories: apparatus-directed behaviors and human-directed behaviors. The former category includes all types of interaction or manipulation of the apparatus (e.g., rubbing, smelling, touching) and head and eye gaze orientation toward it. The human-directed behaviors are categorized as either active (e.g., jumping on the person, pawing to call attention) or passive (e.g., proximity, maintaining close physical contact). Human-directed behaviors might also include gaze or looking back behaviors (e.g.,

from a stationary position, the subject turns/lifts its head toward human faces, without approaching). In order to clarify whether the animal's orientation toward a human may be a request for help, Smith and Litchfield (2013) stressed the importance of using precise terminology and to minimize ambiguous definitions. For example, the behavior of gaze and looking back may be interpreted differently: the first behavior refers to those experimental contexts in which it is possible to observe the direction of the animal's eyes, while in the second case, it is possible only to deduce the orientation of animal's head without seeing its eyes. The gaze alternation between human and apparatus is considered a communication tool and is often used in the analysis of the behavior during the unsolvable task. Other behaviors that can be observed during an unsolvable task are vocalizations (e.g., bark, howl) and stress behaviors (e.g., shaking, yawning, panting, lip-licking).

Results from studies using the impossible task paradigm have demonstrated that specific behaviors, such as physical contact or gaze toward the human, can depend on genetic factors (Persson et al. 2015), likely due to the process of domestication (Miklósi et al. 2003). On the other hand, some investigators have emphasized the role of ontogenesis, showing that the tendency to gaze at humans was positively correlated with age (Passalacqua et al. 2011) and can depend on the type of training that dog received (D'Aniello et al. 2015, Scandurra et al. 2015) or by the living conditions, with kennel dogs gazing less to humans than pet dogs (D'Aniello and Scandurra 2016). Comparative studies suggest that in toddlers and dogs gaze alternation is both an intentional and referential communicative act (Marshall-Pescini et al. 2013).

## Cross-References

- ▶ [Canine Cognition](#)
- ▶ [Decision-Making](#)

- ▶ Problem-Solving
- ▶ Stress
- ▶ Violation of Expectation

## References

- D’Aniello, B., & Scandurra, A. (2016). Ontogenetic effects on gazing behaviour: A case study of kennel dogs (Labrador retrievers) in the impossible task paradigm. *Animal Cognition, 19*, 565–570.
- D’Aniello, B., Scandurra, A., Prato-Previde, E., & Valsecchi, P. (2015). Gazing toward humans: A study on water rescue dogs using the impossible task paradigm. *Behavioural Processes, 110*, 68–73.
- Horn, L., Virányi, Z., Miklósi, Á., Huber, L., & Range, F. (2012). Domestic dogs (*Canis familiaris*) flexibly adjust their human-directed behavior to the actions of their human partners in a problem situation. *Animal Cognition, 15*, 57–71.
- Marshall-Pescini, S., Passalacqua, C., Barnard, S., Valsecchi, P., & Prato-Previde, E. (2009). Agility and search and rescue training differently affects pet dogs’ behaviour in socio-cognitive task. *Behavioural Processes, 78*, 449–454.
- Marshall-Pescini, S., Colombo, E., Passalacqua, C., Merola, I., & Prato-Previde, E. (2013). Gaze alternation in dogs and toddlers in an unsolvable task: Evidence of an audience effect. *Animal Cognition, 16*, 933–943.
- Miklósi, Á., Kubinyi, E., Topál, J., Gácsi, M., Virányi, Z., & Csányi, V. (2003). A simple reason for a big difference: Wolves do not look back at humans, but dogs do. *Current Biology, 13*, 763–766.
- Passalacqua, C., Marshall-Pescini, S., Barnard, S., Lakatos, G., Valsecchi, P., & Prato-Previde, E. (2011). Breed and age group differences in human-directed gazing behaviour. *Animal Behaviour, 82*, 1043–1050.
- Persson, M. E., Roth, L. S. V., Johnsson, M., Wright, D., & Jensen, P. (2015). Human-directed social behaviour in dogs shows significant heritability. *Genes, Brain and Behavior, 14*(4), 337–344.
- Scandurra, A., Prato-Previde, E., Valsecchi, P., & D’Aniello, B. (2015). Guide dogs as model for investigating the effect of life experience and training on gazing behaviour. *Animal Cognition, 18*, 937–944.
- Smith, B. P., & Litchfield, C. A. (2013). Looking back at ‘looking back’: Operationalising referential gaze for dingoes in an unsolvable task. *Animal Cognition, 16*, 961–971.

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# A

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## Approach/Withdrawal Theory

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T(theodore). C. Schneirla (July 23, 1902–August 20, 1968) was among the preeminent comparative psychologists of the twentieth century. An ardent antireductionist, he framed the study of animal behavior and comparative psychology as a holistic, integrative research program (Tobach and Aronson 1970) using both analysis and synthesis (Maier and Schneirla 1935, enlarged in 1964). This program influenced some of the most important comparative psychologists of the twentieth century (e.g., see Aronson et al. 1970). Although those influenced by Schneirla is today a relatively small group (one of the last remaining scientists trained by Schneirla, Ethel Tobach, passed away in 2015 (Greenberg 2015; see also Greenberg, Ethel Tobach, this volume)). Schneirla's ideas continue to influence the thinking of a great many contemporary scientists. Many adhere to his proposal that both psychology and biology are in essence developmental sciences. I also adhere to Schneirla's approach to the study of behavior, an orientation embracing both processes of evolution and development from an epigenetic framework (Lerner and Overton 2013; Michel and Moore 1995; Overton and Lerner 2014).

The focus of this essay is Schneirla's concept of approach/withdrawal which he first introduced in 1939 at a meeting of the American Psychological Association: "This conception envisages negative-positive responses as fundamentally attributable to differential arousal of excitation-reaction systems which function as though they possessed distinctly different activation thresholds. Through natural selection, we may hypothesize the evolution of such mechanisms along adaptive lines. This view has utility as a hypothetical basis for understanding approach-withdrawal behavior in man" (p. 295). In developing this concept Schneirla (1959, 1965) acknowledged being influenced by others including Wundt, Darwin, Jennings, Pillsbury, and his own teacher, J. F. Shepard (Greenberg 1995). Whereas Schneirla identified this concept as a "theory," it is at best a "pragmatic hypothesis" (Bunge 1980, p. 22) although its apparent universal application points to its lawlike character (Greenberg et al. 1991). It is useful to point out that in our still youthful history, psychology can point to no real laws (with the possible exception of the law of effect), and although we use the term theory often, we definitely have none that operate as do those in the older sciences. I direct readers to Uttal's (2005) discussion of what theory is in science and why psychology has none.

Schneirla proposed the A/W concept as a way of understanding the origins of complex behavior in terms of simpler biphasic processes directly related to the quantitative characteristics of

stimuli. “At first, he conceptualized the biphasic processes of approach and withdrawal as related to the state of the organism and the intensity of the effective stimuli, and as critical in the initiation and maintenance of activity. This concept of the biphasic approach-withdrawal concept was expanded later by considering it to be a fundamental feature both in the behavior of simple animals such as protozoa and in early stages of behavioral development of the more complex animal forms” (Tobach and Aronson 1970, p. xvi). Some examples discussed by Schneirla include the consistent lunging forward of many fishes, amphibians, and reptiles to “moving stimuli of small area [and the] snapping responses of toads depend upon quantitative properties of the stimulus” (1959, pp. 311–312); and, “An elementary type of orientation is that in which an animal approaches a low-energy stimulus source, as a neonate kitten nears the abdomen of its mother through crudely directionalized responses to thermal and tactual stimuli from her” (1959, p. 313).

The fundamental premise behind the approach/withdrawal concept is that these response patterns underlie all complex adaptive responses and is a synthesis of several organizing concepts and principles. In their summary of the A/W theory, Raines and Greenberg (1998) described its essential elements: biphasic processes, stimulus intensity, levels of organization, plasticity and epigenesis, and maturation and experience.

*Biphasic processes* (i.e., approach and withdrawal): are characteristic of *all* animals at *all* phyletic levels and are traced to the evolution of adaptive sensory-motor systems – quite simple in lower animals, such as the light-sensitive single cells in earthworms, and complex in vertebrates mediated by the two branches of the autonomic nervous system.

*Stimulus intensity*: low-intensity stimuli elicit approach responses and high-intensity stimuli elicit withdrawal responses. This difference is true throughout the life histories of simple organisms and in the earliest developmental stages of more complex animals. Stimulus intensity refers not only to properties of the external stimulus but also accompanying internal organismic variables, which affect the perception of stimulus intensity

resulting in the dimension of “effective stimulus intensity” (e.g., Helson’s 1964 adaptation level theory).

*Levels of organization* (see Greenberg, Behavioral Levels, this volume): Schneirla’s emphasis on this central organizing principle in science leads to a “psychological way” of understanding behavior in much the same way biologists (e.g., Woodger 1929) invoked the concept to develop a uniquely biological way of thinking. In this way, psychological events are not reducible to biology and physiology. Coupling this idea within the A/W concept provides a basis for identifying the lowest level of organization for adaptive functioning. McGuire and Turkewitz (1979) provided an account of the relationship of Schneirla’s concepts of *effective stimulus intensity* and *levels*.

*Plasticity and epigenesis*: species are increasingly behaviorally plastic at higher phyletic levels, as permitted by increasingly complex nervous systems. Schneirla’s rejection of reductionism and biological determinism enables this increasing behavioral plasticity. Kuo (1967) referred to this as his principle of behavioral potentials, according to which organisms at each behavioral level have the potential to develop species-typical behaviors, although the realization of this potential is the result of the organism’s experiential history and not from their biological endowments (i.e., genes). This rejection of biological reductionism in favor of developmental processes emphasizes that genetic expression is not determined or guaranteed but is probabilistic (e.g., Gottlieb 1970).

*Maturation and experience*: during maturation (i.e., growth and differentiation) the organism is exposed to experiences (all stimulative effects), and it is the *fused* system of maturation and experience (not their interaction) that directs the organism’s behavioral development (Schneirla 1959, 1965). It is, of course, now clear that prenatal endogenous and exogenous stimulation affects behavioral development (Kuo 1967). Gottlieb (2001, p. 2) referred to these types of stimulation as nonobvious experiences. “As for nonobvious experiences, who would have dreamed that squirrel monkeys’ innate fear of snakes derives from their earlier experience with live insects...? Or

that chicks perceiving meal worms as edible morsels is dependent on their having seen their own toes move. . . ?”

Which of these biphasic processes is activated in an organism depends on the stimulus and its intensity. Of course, even identifying just what a stimulus is can be difficult “We often naively assume that ‘the stimulus’ we present to an organism is ‘the same stimulus’ it responds to” (Greenberg et al. 1991, p. 41). As an example, Tronick (1967) showed that a radially decreasing shadow is an effective imprinting stimulus, a result predicted by A/W theory. However, Tronick pointed out that such a stimulus was one that increased in intensity – a decrease in the area of a shadow resulting in a brighter visual intensity. Clearly, the crucial dimension of stimulus intensity depends a great deal on understanding the state of the perceiving organism. McGuire and Turkewitz (1979) distinguished between the objective (physical characteristics) and effective (organismic variables) intensities of a given stimulus. Stimulus intensity is a complex construct and not readily identified in a single modality or by a single physical characteristic. It has been defined in dynamogenic terms (Grice and Hunter 1964) as a dimension dependent on an organism’s adaptation level (Helson 1964). Helson’s mathematical analysis of a stimulus includes its physical characteristics, the state of the organism (including its degree of maturation and developmental level), and other contextual factors, a crucial dimension that Lerner (1989) has termed developmental contextualism. In the phenomenon of imprinting, Moltz (1963) invoked the A/W idea and hypothesized that chicks would imprint to withdrawing objects and not to those which approached. Whereas his data did not support this idea, Bengtson’s (1983) analysis of the complexity of visual stimuli offers an explanation of Moltz’s failure. Bengtson showed that, in imprinting, the intensity of the visual stimulus is a complex function of its angular speed and distance from the eye. Large imprinting objects, then, are not necessarily more intense than smaller ones. What was large or small to Moltz may not have been so to his chicks. Schneirla (1959, 1965) discussed A/W responses in many species and to

many types of stimuli. For example, his 1959 paper “cited the apparent approach to moonlight reflecting from the surf by newly hatched loggerhead turtles at night, the proneness of certain lizards to approach green as opposed to other spectral hues and to approach figures with smooth outlines rather than others with broken outlines” (Greenberg and Haraway 2002, p. 64). Greenberg and Haraway’s discussion of A/W shows it is still an important critical idea in comparative psychology.

### A/W Theory Today

With a single exception – Wolfgang Schleidt’s (Schleidt et al. 2011) continued rejection of Schneirla’s interpretation and his continued support of the Lorenzian ethological interpretation of the Hawk-Goose phenomenon (that young birds flee from a hawk like figure because of an innate recognition of its predatory nature, rather than Schneirla’s (1965) analysis that the shape of a looming predator is a more intense visual stimulus than is the shape of a looming non predator such as a goose) – it is a curious twist of history that the A/W concept has absolutely vanished from use in the animal behavior literature. Of course, Schleidt himself is an ethologist. However, despite a cautionary comment made by the influential developmentalist John Bowlby (1969) soon after Schneirla’s (1965) last extended statement of the A/W concept, that “the extent of its applicability remains unknown” (p. 149), interest in the idea has persisted among developmentalists of all stripes (Hood et al. 1995). While many invoke the concept few acknowledge Schneirla’s influence, as noted by Turkewitz (1987):

By the time his [Schneirla’s] viewpoint had penetrated the realm of developmental psychology it had become, arguably, the dominant position in developmental psychobiology. As such, it tended to be treated by developmental psychologists as a product of the *zeitgeist* or as part of general lore, thus, not requiring attribution. (p.369)

A sampling of contemporary developmentalists working with A/W as formulated by Schneirla are:

**Margaret Sullivan:** work from her research group (e.g., Lewis et al. 2015) has often focused on aspects of emotional behaviors – anger, for example, as expressed by infants in response to blocked goals. This phenomenon is understood to be an approach-related affect. Their work is consistent with “Darwin’s observation that anger leads to behaviors in overcoming obstacles to regain a goal while sadness is a withdrawal emotion as measured related to movement away from the goal. These differential action tendencies are supported by facial behaviors, body activity, and physiological responses such as heart rate and cortisol increases...” (Lewis et al. 2015, p. 1553). Schneirla (1959, 1965), too, indicated that A/W responses apply to the entire organism, from its overt behavior to its covert physiology and neurology.

**Nathan Fox:** Fox’s prolific group often focuses on physiological correlates of temperament (e.g., Helfinstein et al. 2012). Citing earlier work on several animal species they note that biphasic “tendencies across many species suggests that there may be neural circuitry common to many species that is involved in these behaviors. . . [M]ore recent work has extended these findings on approach by focusing on the neural architecture moderating approach-related behavior. Most recently, this work has mapped the relations between individual differences in human temperament and individual differences in neural circuitry function” (p. 818).

Much contemporary work in development, emotion, and temperament frequently refers not to “withdrawal,” as in the Schneirla A/W formulation, but rather to “avoidance.” This focus is the case in the Helfinstein article cited above and others such as Blair et al. (2004), who do not cite Schneirla, although they purport to study approach/withdrawal in preschoolers. They use *avoidance* and *withdrawal* interchangeably. Schneirla was quite clear that his use of *approach* is not the opposite of *avoid*: “Confusion is indicated when the term ‘approach’ is combined with ‘avoid,’ ‘avoid’ as if these were opposite concepts for motivation. . . Seeking and avoidance are of a higher evolutionary and developmental order than

approach and withdrawal, and these terms should not be mismatched” (Schneirla 1959, p. 298).

Another example of this point is Eliot (2006) who does cite Schneirla and thus, presumably, intends to be studying A/W. The term “withdrawal” never appears in his paper and it is clear that he is equating it with “avoidance.” Citing Schneirla (1959), he comments that some have characterized “approach avoidance behavioral decisions as the most critical adaptive judgments that organisms have had to make in the evolutionary past, and it is likely that this adaptive function is the reason that approach-avoidance process are witnessed across animate forms of life...” (p. 113).

Lerner (1989) maintains that when Schneirla and his colleagues articulated the concept of probabilistic epigenesis, they were laying the groundwork for modern developmental theories including the life span perspective in general. This essay is my attempt to outline the essentials of what is surely the most ambitious theoretical endeavor in comparative psychology, past and present. Schneirla began his theory building process in the early stages of his writing. Indeed, his now classic book, *Principles of animal psychology*, co-written with N. R. F. Maier (1934), contains the seeds of the theoretical ideas described in this essay. The principles are postulated to be universal, applying equally to humans and non-humans alike. The “theory,” incomplete as it is, has influenced many researchers across numerous spheres of psychology. Although he was a comparative psychologist, the persistence of his ideas in developmental psychology attests to its enormous significance.

## Cross-References

- ▶ [Behavioral Levels](#)
- ▶ [Comparative Psychology](#)
- ▶ [Development](#)
- ▶ [Ethel Tobach](#)
- ▶ [Evolution](#)



## References

- Aronson, L. R., Tobach, E., Lehrman, D. S., & Rosenblatt, J. S. (Eds.). (1970). *Development and evolution of behavior: Essays in memory of T. C. Schneirla*. San Francisco: Freeman.
- Bengston, H. (1983). The approach and preference behavior of chicks in relation to the intensity of neural-input effects. *Animal Behaviour*, *31*, 490–496.
- Blair, C., Peters, R., & Granger, D. (2004). Physiological and neuropsychological correlates of approach/withdrawal tendencies in preschool: Further examination of the behavioral inhibition system/behavioral activation system scales for young children. *Developmental Psychobiology*, *45*, 113–124.
- Bowlby, J. (1969). *Attachment and loss: vol 1. Attachment*. London: Hogworth Press.
- Bunge, M. (1980). *The mind-body problem*. Oxford: Pergamon.
- Elliot, A. J. (2006). The hierarchical model of approach-avoidance motivation. *Motivation and Emotion*, *30*, 111–116.
- Gottlieb, G. (1970). Conceptions of prenatal behavior. In L. R. Aronson, E. Tobach, D. S. Lehrman, & J. S. Rosenblatt (Eds.), *Development and evolution of behavior: Essays in memory of T. C. Schneirla* (pp. 111–137). San Francisco: W. H. Freeman.
- Gottlieb, G. (2001). The relevance of developmental-psychobiological metatheory to developmental neuropsychology. *Developmental Neuropsychology*, *19*, 1–9.
- Greenberg, G. (1995). The historical development of the approach/withdrawal concept. In K. E. Hood, G. Greenberg, & E. Tobach (Eds.), *Behavioral development: Concepts of approach/withdrawal and integrative levels* (pp. 3–17). New York: Garland.
- Greenberg, G. (2015). In Memoriam: Ethel Tobach (1921–2015). *American Psychologist*, *71*, 75.
- Greenberg, G., & Haraway, M. M. (2002). *Principles of comparative psychology*. Boston: Allyn and Bacon.
- Greenberg, G., McCarthy, T., & Radell, P. (1991). Approach/withdrawal theory and the concept of stimulus intensity (complexity). *Journal of Psychology and the Behavioral Sciences*, *6*, 40–48.
- Grice, G. R., & Hunter, J. J. (1964). Stimulus intensity effects depend upon the type of experimental design. *Psychological Review*, *71*, 247–256.
- Helfinstein, S. M., Fox, N. A., & Pine, D. S. (2012). Approach-withdrawal and the role of the striatum in the temperament of behavioral inhibition. *Developmental Psychology*, *48*, 815–826.
- Helson, H. (1964). *Adaptation-level theory*. New York: Harper & Row.
- Hood, K. E., Greenberg, G., & Tobach, E. (Eds.). (1995). *Behavioral development: Concepts of approach/withdrawal and integrative levels*. New York: Garland.
- Kuo, Z.-Y. (1967). *The dynamics of behavior development: An epigenetic view*. New York: Plenum Press.
- Lerner, R. M. (1989). Developmental contextualism and the life-span view of person-context interaction. In M. H. Bornstein & J. S. Bruner (Eds.), *Interaction in human development* (pp. 219–239). Hillsdale: Lawrence Erlbaum.
- Lerner, R. M., & Overton, W. F. (2013, June 1). Epigenetics, evolution and embodiment: On the conceptual vacuity of evolutionary psychology. *OA Genetics*, *1*(1), 6.
- Lewis, M., Sullivan, M. W., & Kim, H. M.-S. (2015). Infant approach and withdrawal in response to a goal blockage: Its antecedent causes and its effect on toddler persistence. *Developmental Psychology*, *51*, 1553–1563.
- Maier, N. R. F., & Schneirla, T. C. (1964). *Principles of animal psychology* (Enlarged ed.). New York: Dover.
- McGuire, I., & Turkewitz, G. (1979). Approach-withdrawal theory and the study of infant development. In M. Bortner (Ed.), *Cognitive growth and development: Essays in memory of Herbert G. Birch* (pp. 57–85). New York: Brunner/Mazel.
- Michel, G. F., & Moore, C. L. (1995). *Developmental psychobiology*. Cambridge, MA: MIT Press.
- Moltz, H. (1963). Imprinting: An epigenetic approach. *Psychological Review*, *70*, 123–138.
- Overton, W. F., & Lerner, R. M. (2014). Fundamental concepts and methods in developmental science: A relational perspective. *Research in Human Development*, *11*, 63–73.
- Raines, S., & Greenberg, G. (1998). Approach/withdrawal “theory”. In G. Greenberg & M. Haraway (Eds.), *Comparative psychology: A handbook* (pp. 74–80). New York: Garland Publishing.
- Schleidt, W., Shalter, M. D., & Moura-Neto, H. (2011). The hawk/goose story: The classical ethological experiments of Lorenz and Tinbergen, revisited. *Journal of Comparative Psychology*, *125*(2), 121–133.
- Schneirla, T. C. (1939). A theoretical consideration of the basis for approach-withdrawal adjustments in behavior. *Psychological Bulletin*, *37*, 501–502. Reprinted in L. R. Aronson, E. Tobach, D. S. Lehrman, & J. S. Rosenblatt (Eds.) (1972), *Selected writings of T. C. Schneirla* (pp. 295–296). San Francisco: Freeman.
- Schneirla, T. C. (1959). An evolutionary and developmental theory of biphasic processes underlying approach and withdrawal. In M. R. Jones (Ed.), *Nebraska symposium on motivation, Vol. 7*. Lincoln: University of Nebraska Press. Reprinted in L. R. Aronson, E. Tobach, D. S. Lehrman, & J. S. Rosenblatt (Eds.), *Selected writings of T. C. Schneirla*. San Francisco: Freeman.
- Schneirla, T. C. (1965). Aspects of stimulation and organization in approach-withdrawal processes underlying vertebrate behavioral development. In D. S. Lehrman, R. Hinde, & E. Shaw (Eds.), *Advances in the study of behavior, Vol. 1* (pp. 1–71). New York: Academic Press. Reprinted in L. R. Aronson, E. Tobach, D. S. Lehrman, & J. S. Rosenblatt (Eds.). (1972). *Selected writings of T. C. Schneirla* (pp. 345–382). San Francisco: Freeman.
- Tobach, E., & Aronson, L. R. (1970). T. C. Schneirla: A biographical note. In L. R. Aronson, E. Tobach, D. S. Lehrman, & J. S. Rosenblatt (Eds.), *Development and*

- evolution of behavior: Essays in memory of T. C. Schneirla* (pp. xi–xviii). San Francisco: Freeman.
- Tronick, E. (1967). Approach response of domestic chicks to an optical display. *Journal of Comparative and Physiological Psychology*, 64, 529–531.
- Turkewitz, G. (1987). Psychobiology and developmental psychology: The influence of T. C. Schneirla on human developmental psychology. *Developmental Psychobiology*, 20(4), 369–375.
- Uttal, W. R. (2005). *Neural theories of mind: Why the mind-brain problem may never be solved*. Mahwah: Erlbaum.
- Woodger, J. H. (1929). *Biological principles*. London: Routledge & Kegan Paul, Ltd. Reprinted with new introduction, 1967.

# E

## Entopallium

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### Synonyms

[Avian](#); [Discrimination learning](#); [Ectostriatum](#);  
[Memory](#); [Vision](#)

### Introduction

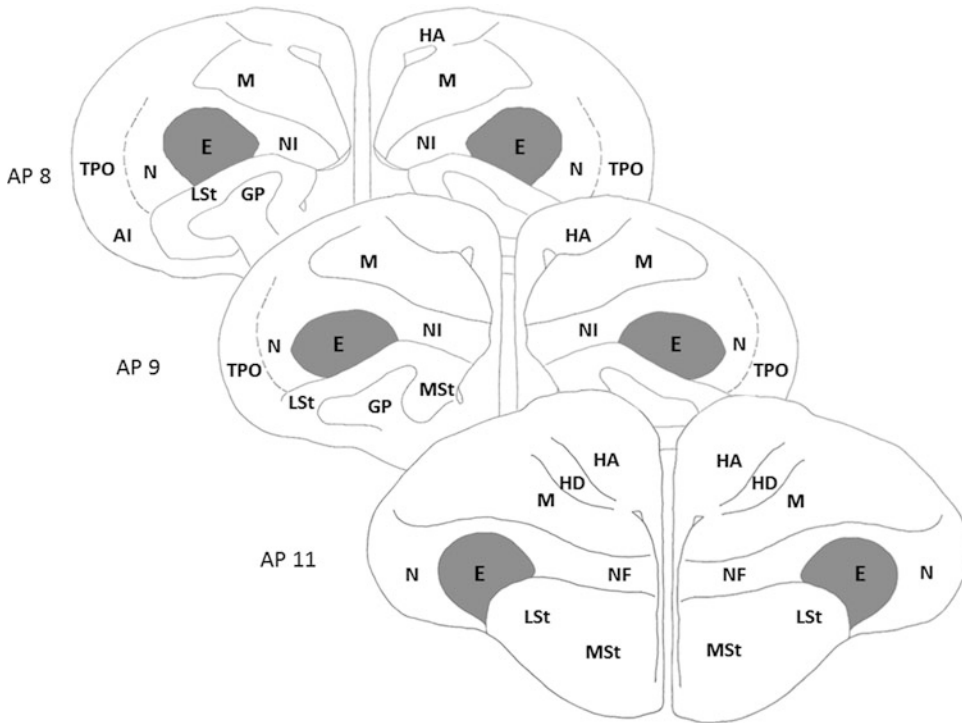
The dorsal ventricular ridge (DVR) is the main body of mass that forms the avian telencephalon. The DVR contains the major pallial regions of the avian brain, including the nidopallium (N), mesopallium (M), arcopallium (A) and, nested among these areas, the entopallium (E). Based on its afferent and efferent projections, the effects of lesions to the area, and single-unit electrophysiological data, the E is a higher-order visual and motion processing structure, and is considered analogous to some region of the primate extrastriate cortex.

### Anatomy of Entopallium

In most avian species, the E is a large curved structure located deep within the DVR,

surrounded by the N in all but the ventral position (Fig. 1). Depending on the posterior (AP8) to anterior (AP11) position, dorsal to the E is the M, hyperpallium densocellulare (HD), and hyperpallium apicale (HA). Ventral to the E is lateral striatum (LSt), globus pallidus (GP), and medial striatum (MSt) (Reiner et al. 2004). The E is a component of one of the two main pathways that transmit information to the telencephalon in the avian brain. The thalamofugal pathway projects from the retina to the nucleus opticus principalis thalami (OPT), and then to a region of the dorsal telencephalon known as the visual Wulst (HA and HD). The tectofugal pathway, on the other hand, projects from the retina to the optic tectum (TeO), then bilaterally to the nucleus rotundus (Rt), and finally ipsilaterally to the E (Fig. 2; Krützfeldt and Wild 2005). The consensus from studies examining the projections from Rt to the E is that the projections are organized topographically along the anterior–posterior axis, such that neurons in the anterior Rt project to anterior E, while neurons in the posterior Rt projects to posterior E.

The E can be divided into two main subregions, the core (Ec) and the peripheral belt (Ep), with Ep surrounding Ec (Karten and Hodos 1970). In the zebra finch, the outer boundary of E is clearly defined; however, in the pigeon, the boundary appears intermittent. The cells in the two subregions can be differentiated on the basis of a number of characteristics, as well as their projection patterns. With respect to cell characteristics, Ec is populated mainly with medium-sized



**Entopallium, Fig. 1** Cross section through the pigeon brain demonstrating the location of the E (shaded grey). The following are the brain regions as defined by Reiner et al. (2004). *AI* arcopallium intermedium, *E* entopallium, *GP* globus pallidus, *HA* hyperpallium apicale, *HD*

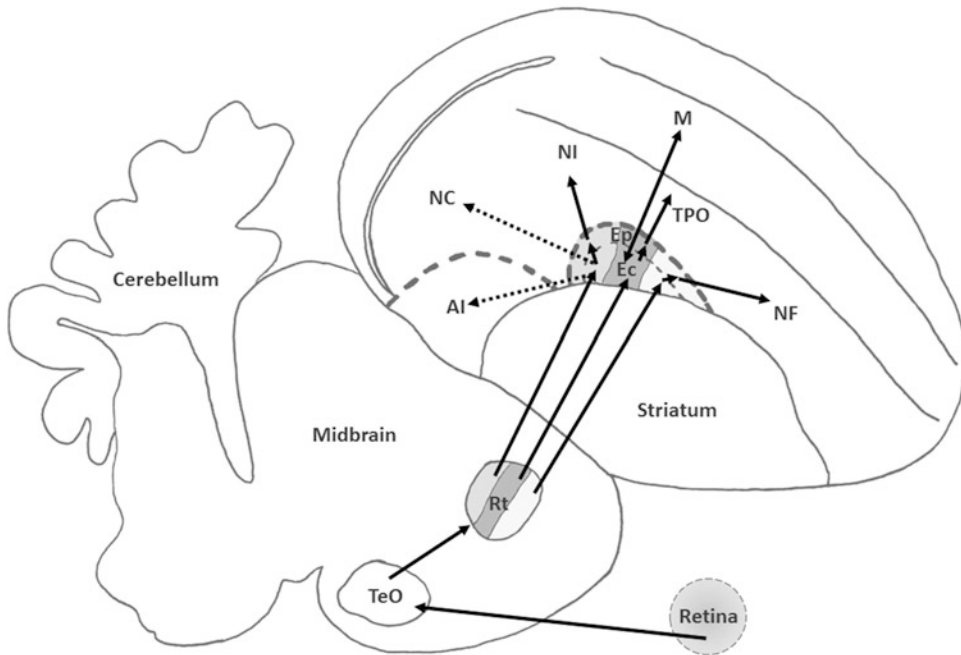
hyperpallium densocellulare, *LSt* lateral striatum, *M* mesopallium, *MSt* medial striatum, *N* nidopallium, *NF* nidopallium frontale, *NI* nidopallium intermedium, *TPO* temporo-parieto-occipitalis

round cells with thick myelinated axons that are generally parvalbumin (PV) positive. In contrast, Ep neurons are characterized by smaller and longer cells with thin myelinated axons, very few of which are PV-positive, the exception being the zebra finch, which has a greater number of PV-positive cells in area Ep.

With respect to afferent and efferent projections, the major projections from Ec are primarily directed to Ep and then onto Ep2 (Fig. 2), an ill-defined area immediately surrounding the Ep and that some consider similar to Ep (Krützfeldt and Wild 2005). For the current entry, Ep2 is considered to be coextensive with Ep. Much like the projections to the E from Rt, the projections from Ec to Ep, and from Ep to other pallial regions of the avian brain are also arranged in a topographical manner along the anterior–posterior axis, such that projections from the anterior portion of Ep are sent to nidopallium frontale (NF),

projections from the intermediate regions of Ep to temporo-parieto-occipitalis (TPO), and projections from posterior regions of Ep to nidopallium intermedium (NI). Along with the major projections from Ep, there are minor projections from the posterior regions of Ec to arcopallium intermedium (AI) and nidopallium caudale (NC).

Although the majority of projections to the pallial regions of the avian brain originate from Ep, there are minor projections from Ec to the NF, TPO, and NI as well (Krützfeldt and Wild 2005). In the zebra finch and chickens, Ec also projects to the lateral striatum (LSt), and Ec may also have reciprocal projections with the M in both the zebra finch and pigeon (Krützfeldt and Wild 2005).



**Entopallium, Fig. 2** The afferent and efferent projection patterns of the E. The E is part of the tectofugal pathway. Information flows from the retina to TeO, then to the Rt, and from there in a topographical fashion to Ec. From Ec, information projects to Ep and then the rest of the avian pallium. *Arrows in solid line* represent major projection patterns, while *dashed arrows* represent minor projection patterns, with all arrow points indicating the direction of

the projection. Regions shaded in Rt and E represent the anterior, intermediate, and posterior divisions of each area. The following are the brain regions as defined by Reiner et al. (2004). *AI* arcopallium intermedium, *Ec* entopallium core, *Ep* entopallium peripheral belt, *M* mesopallium, *NC* nidopallium caudale, *NF* nidopallium frontale, *NI* nidopallium intermedium, *Rt* nucleus rotundus, *TeO* optic tectum

### Functions of Entopallium: Lesion Studies

Hodos and his many colleagues extensively explored the functions of the E in a series of psychophysical discrimination studies conducted throughout the 1970s and 1980s (see Hodos et al. 1988, and references therein). Damage to the E causes a variety of visual impairments. In one study, birds were trained to discriminate between a blank uniform stimulus and stimuli with different spatial frequency gratings. After E lesions, the birds showed impairments in visual acuity, that is, elevated thresholds for detecting gratings. E lesions also cause elevated luminous intensity thresholds. Similarly, E lesions, especially medial E lesions, cause elevated thresholds for detecting differences in the size of an annulus, a measure of low spatial frequency. Hodos and colleagues suggested that the medial E processes information

about the low-spatial-frequency structure of stimuli, whereas the lateral E processes information about the high-spatial-frequency structure of stimuli.

Damage to the E also causes impairments beyond elevated psychophysical thresholds, such as in the processing of complex visual information. For example, Bessette and Hodos (1989) reported that pigeons with E damage show marked deficits in the ability to discriminate between different patterns (e.g., vertical vs. horizontal line, or triangle with apex at top vs. triangle with apex at bottom) and intensities (two squares that differed in luminance), but not colors (green vs. yellow). Additionally, others have reported that E lesions cause impairments in the ability to discriminate between a number of different mirror-image and non-mirror-image stimuli that were matched on the basis of luminance. The most

striking impairments after E lesions are in the ability to discriminate lateral mirror images, and this does not seem to be a function of difficulty, as the lateral-mirror-image discrimination was acquired preoperatively at the same rate as the other mirror-image and non-mirror-image discriminations.

Watanabe (1996, and references therein) conducted a series of studies in the 1990s examining the role of the E in the processing of ecologically relevant and ecologically irrelevant stimuli. Lesions of the E does not impair the ability to discriminate food items (corn, peas, buckwheat, and wheat) from nonfood items (stones, twigs, nuts, and yellow paper clips), but does impair the ability to discriminate these stimuli when they were randomly arranged into two groups (e.g., corn, peas, stones, and twigs vs. buckwheat, wheat, nuts, and yellow paper clips), a finding that likely reflects the fact that the randomly arranged discrimination is harder than the food versus nonfood discrimination. Similarly, E lesions impair the ability to discriminate between many exemplars of a triangle versus many exemplars of a line, but has little effect on the ability to discriminate between one triangle and one line.

E lesions also cause an impairment in the ability to discriminate one pigeon from another pigeon, but does not impair the ability to discriminate one pigeon from another bird such as a quail. Although such a finding might reflect the fact that the E is important for discriminating members of one's own species from another, again it could also reflect task difficulty, with the pigeon versus pigeon discrimination more difficult and hence more sensitive to E lesions than the pigeon versus quail discrimination. Indeed, the effect of task difficulty was confirmed when in a follow-up study Watanabe (1996) showed that E lesions also cause impairments in the ability to discriminate between a sparrow and a starling, but not between pigeons and other birds. Also related to task difficulty is the finding that E lesions do not impair the acquisition of color discrimination (yellow vs. green) but does impair subsequent reversals of the color discrimination.

In some of the aforementioned lesion studies, the impairments are correlated with the extent of

damage to  $E_c$ , whereas in other studies what seems important is the total extent of the lesion to the E. As of yet, no firm functional differentiation has been uncovered for the core versus the belt regions. Some, however, report functional differences within different regions of the E as a whole. The earlier reported study by Hodos and colleagues, for example, proposed functional differences between the medial and lateral E with respect to the processing of low- and high-spatial frequency information. Nguyen et al. (2004) also report functional differentiation within the E. Birds were trained on a psychophysical procedure to perform either a pattern discrimination or motion discrimination, both with varying degrees of background noise superimposed upon the images. The authors uncovered a double dissociation, with birds with rostral E lesions impaired on the pattern discrimination and not the motion discrimination, whereas birds with caudal E lesions impaired on the motion discrimination and not the pattern discrimination. The findings of both pattern and motion impairments following lesions to the E suggests that it may serve functions similar to the primate's extrastriate cortex, which houses areas responsible for both pattern perception (e.g., inferior temporal cortex) and motion perception (e.g., area MT).

### **Functions of Entopallium: Electrophysiological Studies**

Early studies reported that cells in the E display characteristics similar to those reported in extrastriate visual cortex of primates (see Colombo et al. 2001, and references therein). For example, compared to the receptive fields of neurons in visual Wulst and primate striate cortex, the receptive fields of neurons in the E and primate extrastriate cortex are generally large. Similarly, the receptive fields of cells in visual Wulst and striate cortex are retinotopically mapped, whereas those in the E and extrastriate cortex show little retinotopic mapping.

Beyond the small number of studies characterizing the basic properties of E neurons, however, few electrophysiological studies have been



conducted. Those that have been conducted further add to the view that the E represents a higher-order visual processing region in the avian brain similar to the primate extrastriate cortex. Using a variety of differently shaped and colored stimuli that included pictures of pigeons, Scarf et al. (2016) reported that over 90% of E neurons are visually responsive and 20% show selective activity for one or more of the tested stimuli, numbers higher than any of the other three areas examined (nidopallium, arcopallium, and hippocampus), and numbers that are not only in line with extrastriate regions of the primate brain, but are representative of what one might expect from a higher-order visual area. Some neurons in the E are also selective for the size, speed, or direction of stimulus movement, a trend thought to be associated with the large receptive fields found in the E. The findings of neurons responsive to shape and motion further add to the view that the E serves a similar function to the primate extrastriate cortex.

The E is also involved in memory for visual information. According to Johnston et al. (2017, and references therein), 70–85% of E neurons display activity during the delay period of a delayed matching-to-sample task when the animals are required to remember visual information. Additionally, E neurons are more likely to display delay activity when the pigeons are completing the task at high (>75% correct) compared to low (<75% correct) performance levels. Johnston et al. (2017) also report that delay activity remained stable throughout the delay period. The finding of delay neurons, that encountering delay neurons is more likely when the animal is performing well as opposed to poorly, and the fact that delay activity remains stable throughout the delay period, parallel the characteristics of memory cells found in the primate extrastriate cortex.

## Conclusion

The E is the pallial termination point of the tectofugal pathway. From the E, information is distributed throughout the rest of the avian brain. The E is primarily a visual structure and damage

leads to impairments in visual acuity, brightness discrimination, size discrimination, as well as the ability to discriminate different shapes and naturalistic objects. Damage to the E also causes impairments in motion perception. There is little evidence at present to support a functional difference between the core and belt regions, although there is some evidence for functional differentiation along the medial and lateral extent of the E, and in particular between the rostral and caudal extent of the E, with the rostral area being more involved in pattern discrimination and the caudal area more involved in motion discrimination. The E may also play a role in visual memory and cognition. On the basis of projection patterns, the effects of lesions, and findings from electrophysiological studies, the E has functions similar to regions of the primate extrastriate cortex.

## Cross-References

- ▶ [Afferent and Efferent Impulses](#)
- ▶ [Cognition](#)
- ▶ [Comparative Cognition](#)
- ▶ [Concept Formation](#)
- ▶ [Declarative Memory](#)
- ▶ [Delayed Match-to-Sample](#)
- ▶ [Discrimination Learning](#)
- ▶ [Dorsal Ventricular Ridge \(Dvr\)](#)
- ▶ [Episodic Memory](#)
- ▶ [Instrumental Learning](#)
- ▶ [Learning](#)
- ▶ [Lesion](#)
- ▶ [Matching](#)
- ▶ [Matching-to-Sample](#)
- ▶ [Memory](#)
- ▶ [Natural Categories](#)
- ▶ [Neural Impulse](#)
- ▶ [Neuron](#)
- ▶ [Operant Chamber](#)
- ▶ [Pattern Learning](#)
- ▶ [Pigeon](#)
- ▶ [Reinforcement](#)
- ▶ [Retention](#)
- ▶ [Reversal Learning](#)
- ▶ [Skinner Box](#)
- ▶ [Vision](#)

- ▶ Visual Recognition
- ▶ Working Memory

## References

- Bessette, B. B., & Hodos, W. (1989). Intensity, color, and pattern discrimination deficits after lesions of the core and belt regions of the ectostriatum. *Visual Neuroscience*, *2*, 27–34. doi:10.1017/S0952523800004296.
- Colombo, M., Frost, N., & Steedman, W. (2001). Responses of ectostriatal neurons during delayed matching-to-sample behavior in pigeons (*Columba livia*). *Brain Research*, *917*, 55–66. doi:10.1016/S0006-8993(01)02906-7.
- Hodos, W., Weiss, S. R. B., & Bessette, B. B. (1988). Intensity difference thresholds after lesions of ectostriatum in pigeons. *Behavioural Brain Research*, *30*, 43–53. doi:10.1016/0166-4328(88)90007-1.
- Johnston, M., Anderson, C., & Colombo, M. (2017). Neural correlates of sample-coding and reward-coding in the delay activity of neurons in the entopallium and nidopallium caudolaterale of pigeons (*Colombo livia*). *Behavioural Brain Research*, *317*, 382–392. doi:10.1016/j.bbr.2016.10.003.
- Karten, H. J., & Hodos, W. (1970). Telencephalic projections of the nucleus rotundus in the pigeon (*Columba livia*). *Journal of Comparative Neurology*, *140*, 35–51. doi:10.1002/cne.901400103.
- Krützfeldt, N. O. E., & Wild, J. M. (2005). Definition and novel connections of the entopallium in the pigeon (*Columba livia*). *Journal of Comparative Neurology*, *490*, 40–56. doi:10.1002/cne.20627.
- Nguyen, A. P., Spetch, M. L., Crowder, N. A., Winship, I. R., Hurd, P. L., & Wylie, R. W. (2004). A dissociation of motion and spatial-pattern vision in the avian telencephalon: Implications for the evolution of “visual streams”. *Journal of Neuroscience*, *24*, 4962–4970. doi:10.1523/JNEUROSCI.0146-04.2004.
- Reiner, A., Perkel, D. J., Bruce, L. L., Butler, A. B., Csillag, A., Kuenzel, W., Medina, L., Paxinos, G., Shimizu, T., Striedter, G., Wild, M., Ball, G. F., Durand, S., Güntürkün, O., Lee, D. W., Mello, G. V., Powers, A., White, S. A., Hough, G., Kubikova, L., Smulders, T. V., Kazuhiro, W., Dugas-Ford, J., Husband, S., Yamamoto, K., Yu, J., Siang, C., & Jarvis, E. D. (2004). Revised nomenclature for avian telencephalon and some related brainstem nuclei. *The Journal of Comparative Neurology*, *473*(3), 377–414. doi:10.1002/cne.20118.
- Scarf, D., Stuart, M., Johnston, M., & Colombo, M. (2016). Visual response properties of neurons in four areas of the avian pallium. *Journal of Comparative Physiology A*, *202*, 235–245. doi:10.1007/s00359-016-1071-6.
- Watanabe, S. (1996). Effects of ectostriatal lesions on discrimination of conspecific, species and familiar objects in pigeons. *Behavioural Brain Research*, *81*, 183–188. doi:10.1016/S0166-4328(96)89079-6.

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# B

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## Behaviorism

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### Introduction

Psychology initially lacked objectivity, and thus it was difficult to label it as a science. Drawing on Wilhelm Wundt and Edward Titchener's works, psychology was focused on examining one's consciousness through introspection. Psychologists at the time were not concerned with observable behavior but rather mental states such as thoughts and feelings. From this, assumptions were made as to how the mind organizes information, the factors that affect the mind, and the structure of the mind. Sigmund Freud contributed to this mentalistic approach by focusing on internal conflicts that take place in the unconscious mind and how these unresolved conflicts could lead to psychopathology. Freud's work spread quickly and took a stronghold in Europe. Many psychologists in the United States believed in Freud's work, but there were a few who wanted psychology to return to a science, including John Watson.

John Watson founded behaviorism with the goal to scientifically study human behavior (Watson 1913). The primary goals of behaviorism are to predict and control behavior, with the secondary goals focusing on a scientific and objective approach to measuring and explaining behavior.

This movement led to the scientific advancement of psychology as theories, methodologies, and its applications began to rely on objectivity.

As psychology was advancing, so was behaviorism. There are three stages of behaviorism: associationism (1897–1930), neobehaviorism (1930–1960), and sociobehaviorism (1960–Present). Together, these three schools of thought informed research and its application in psychology.

### Associationism

The associationism period formally began in 1870, but learning by association was discussed more than 2000 years ago by Aristotle (Schultz and Schultz 2016). Aristotle suggested that humans learn by associating an object and a response together. Aristotle's work was revisited by the British associationists, British philosophers, especially by John Locke and David Hume. They spoke about how associations could lead to reflexive responses, particularly as the strength of the association increased (Schultz and Schultz 2016). Locke referred to humans' minds as *tabula rasa*, meaning blank slate. He believed human beings are born without knowledge and that all learning occurs as a result of their experiences. Hume argued that all thoughts are a result of the individual's experience, specifically the individual's impression of a stimulus determines their ideas. This is to say, the individual does not have unique thoughts, but rather his thoughts are

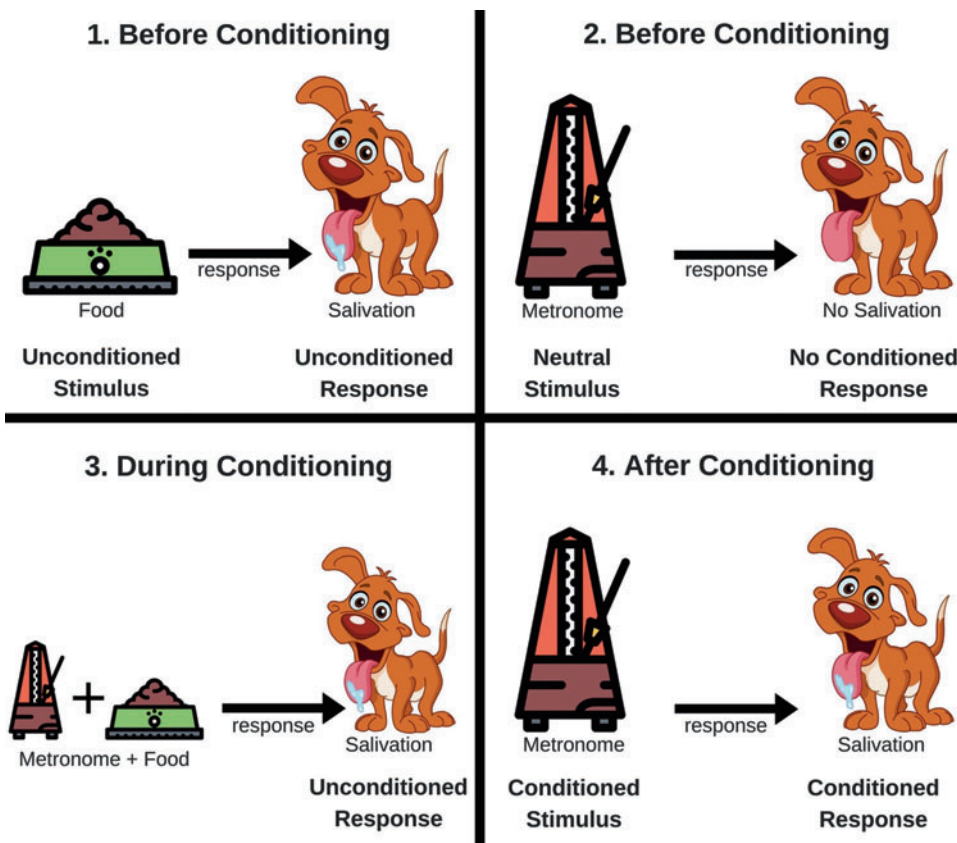
dictated by linking impressions and ideas learned in his experience. These links are solidified through resemblance, contiguity, and cause and effect (Hume 1740/2012). While Hume's ideas about solidifying the relationship between impression and ideas were found to be true, there was no scientific evidence for this at the time.

Ivan Pavlov's (1849–1936) work on *classical conditioning* was the first scientific support for associations. Pavlov, a Russian physiologist, noticed that immediately before he went to feed his dogs, they were already salivating; it was almost as if they knew they were going to be fed. Being an effective scientist, Pavlov systematically examined this behavior. Pavlov's typical experiment involved a dog in a dark room. A light would turn on, and 30 s later, food was presented, eliciting the salivation response (Pavlov 1928). This pairing occurred several times and resulted

in the dog salivating once the light was presented, even if the food was not presented. Pavlov showed that the dog was conditioned to salivate when the light was turned on.

In classical conditioning terms (Pavlov 1928), the food is known as an unconditioned stimulus (US). The unconditioned response (UR) is when the dog automatically salivates as the food is presented. The light begins as a neutral stimulus (NS) and as it is repeatedly paired with the US, the light becomes known as the conditioned stimulus (CS). The repeated pairing of the US and CS conditions a dog to salivate when the room is lit, the conditioned response (CR; see Fig. 1).

Another common example of classical conditioning (aka respondent conditioning) that Pavlov studied was teaching a dog to salivate to the sound of a metronome. The sound of a metronome begins as a NS, as it does not originally produce a response.



Behaviorism, Fig. 1 Classical conditioning

Presenting food, the US, elicits a salivation response/reflex, a UR, from the dog. If the experimenter were to present the metronome and then shortly afterward present the food, the dog would salivate. After several trials, the sound of the metronome, the CS, becomes paired with food, and the dog elicits a salivation response, CR, even when just the metronome is presented. Take note that in both examples, the CS was presented *shortly before* the US. Studies have shown that conditioning a response when the CS is presented after the US is not very effective (Pavlov 1927). In fact, conditioning occurs most rapidly when the CS is presented one-half second before the US.

Throughout his work, Pavlov founded several principles of conditioning, such as extinction, stimulus generalization, stimulus discrimination, and higher-order conditioning.

### Extinction

A CS can cease to produce a CR if the CS is repeatedly presented alone. By repeatedly presenting the light without the food, the dog learns to not salivate. This process is known as *extinction* (Pavlov 1927, 1928). Pavlov found that even when the CR seems to be extinguished, it is possible for the CR to reappear after the CS has not been presented for some time. Pavlov labeled this *spontaneous recovery* (Pavlov 1927, 1928). Let's use the example above. A dog is trained to salivate when light is paired with food, but after several trials of presenting the CS alone, the dog no longer salivates. If a delay of several hours is administered before the next presentation of the CS, the dog is likely to produce the CR, even though the CS and the US were not paired together. Spontaneous recovery can be extinguished by repeatedly presenting the CS without the US. If the CS and US were occasionally paired together during this process, it would only strengthen the association.

### Stimulus Generalization and Discrimination

In most classical conditioning experiments, only two stimuli are paired together, the CS and the US; however, the CR will be elicited not just from the CS but also from similar stimuli to the CS. The more similar a stimulus is to the CS, the more

likely it will elicit the CR. This process is known as *stimulus generalization* (Pavlov 1928). Let's refer back to Pavlov's prototypical study where he paired a metronome (CS) with food (US), causing the dog to salivate. After several pairings, the dog is likely to salivate to the stimuli resembling the sound of the metronome, such as wind chimes, a doorbell, or hitting a glass with a utensil. The dog is not likely to salivate to sounds that do not sound like a metronome, such as dropping a book on the floor, making a cup of coffee, or a siren wailing. This ability to differentiate between the CS and other stimuli, and not produce the CR, is known as *stimulus discrimination* (Pavlov 1928). Pavlov could enhance the dog's ability to discriminate between the CS and other stimuli by deliberately pairing the metronome with food and then present another tone without the food. The dog will begin to discriminate between the two tones and respond just to the CS.

### Higher-Order Conditioning

Pavlov took his research one step further by demonstrating that once a dog was fully conditioned to a CS, he could then pair the CS with a new NS. The previous CS takes the place of the US and is known as a first-order CS. This process is called *higher-order conditioning* (Pavlov 1928). For example in second-order conditioning, Pavlov trained a dog to salivate to a metronome (the first-order CS) and then paired it with a black square (the new CS), to teach the dog to salivate at the sight of a black square. Pavlov found in some instances third-order conditioning could be derived; however, he could never surpass third-order conditioning.

### John Watson

Pavlov's work on classical conditioning became more influential when John Watson made it the bedrock of his theory, behaviorism. Watson was not happy with the direction of psychology, as he viewed it to be unsystematic. In 1913, Watson published the article "Psychology as the Behaviorist Views It," commonly known as the "Behaviorist Manifesto." Watson proposed that a behaviorist views psychology as a purely objective science, concerned with only what is

observable and objectifiable. This was contrary to mainstream psychology of Watson's time. Most psychologists believed in introspection and consciousness. Watson rejected these terms because they were not observable and could not be empirically validated. He treated psychology as a science and promoted operationalism through clearly defining terms and observing behaviors. This branch of behaviorism is known as *methodological behaviorism*.

Watson envisioned behaviorism as the *prediction* and *control* of behavior based on sound scientific methods. Watson and Rayner (1920) demonstrated this through classical conditioning. In his famous experiment, Watson took a 1-year-old boy named Little Albert and conditioned him to be afraid of a white rat. Watson first measured Albert's baseline by observing Albert's physical response when he was presented with a white rat, rabbit, dog, monkey, seal fur coat, Santa Claus mask, and fire. Albert had a positive response to these stimuli, according to Watson's report. Watson then presented a white rat to Albert while simultaneously hitting a steel bar with a hammer. The loud noise was an aversive stimulus to Albert. Watson repeated the pairing several times and Albert began to cry. Watson then presented the rat alone and it evoked a fear response, known as a *conditioned emotional response*. Albert's fear response of crying and crawling away from the stimulus generalized to animals and objects like a white rat (e.g., rabbit, fur coat, Santa Claus mask). An example of stimulus discrimination, Albert did not emit a fear response when presented with a monkey, as the monkey did not resemble the white rat (Watson and Rayner 1920).

Watson never cured Albert's conditioned fear response, as Albert's mother and him moved at the end of the experiment. In 1924, Mary Cover Jones worked on her dissertation under the supervision of John Watson and provided methodological behaviorism with the first glimpse of applied research and a treatment approach. She tested a variety of methods to eliminate the fears (e.g., frogs, fish, rabbits, rats) of a 3-year-old boy named Peter, most notably systematic desensitization and modeling (discussed in detail later in the chapter). Cover Jones drew on Pavlov's and

Watson's works on how conditioned emotional responses form. She recognized that Peter learned to associate rabbits as an aversive stimulus and, therefore, avoided rabbits. Cover Jones decided to recondition Peter by incrementally exposing him to a rabbit with an appetitive stimulus present. Cover Jones placed Peter in a high chair with his snack (an appetitive stimulus) and positioned a caged rabbit across the room. Initially, Peter expressed fear, but after several presentations, the fear response subsided. The following day, Cover Jones brought the caged rabbit within 12 ft. of Peter as he was snacking, which was just enough to evoke a slight arousal from Peter. She repeated this process for several days, each time bringing the rabbit closer and closer to Peter. She eventually let the rabbit out of its cage and had Peter touch the rabbit. The last two steps in this hierarchy were to have Peter fondle the rabbit affectionately and then to let the rabbit nibble his fingers (Cover Jones 1924). This study is the beginning of *systematic desensitization*, which is still commonly used to treat anxiety.

### Behavior Therapy

Cover Jones's work on systematic desensitization earned her the title "Mother of Behavior Therapy." Her work went largely unnoticed until Joseph Wolpe, a psychiatrist from South Africa, formalized the treatment approach (Wolpe 1958). In 1944, Wolpe was working as a military medical officer and found psychoanalysis to be ineffective in treating "war neurosis"; as such, when he returned from the war, he began to research an effective way to treat neuroses. Using cats as his subjects, he placed them in a cage and shocked them repeatedly until it produced an anxious response. Trying to cure this response, Wolpe attempted several unsuccessful methods, including no longer shocking the cats when they were in the cage. What he did find to be effective was to leave the cats in a *slightly* anxiety-producing situation (e.g., shocking them) to the point where they would still eat. Wolpe would repeat these exercises, gradually increasing the intensity. The cats eating while anxious is an example of *reciprocal inhibition* or counterconditioning (Wolpe 1958). Reciprocal inhibition is the process where



an organism cannot be relaxed and tensed simultaneously, and, therefore, the feeling of anxiety can be *counterconditioned* if the organism performs a relaxing behavior (e.g., eating). In Wolpe's study, the cats eating inhibited the cats' anxiety.

Wolpe created four steps for systematic desensitization in humans: diagnose the patient, construct a hierarchy, teach relaxation, and conduct therapy sessions (Wolpe 1958). The first step was to examine the presenting problem and provide a correct diagnosis. Then, the therapist and patient created a hierarchy of anxiety-producing situations ranging from least anxiety producing (0) to most anxiety producing (100). Wolpe found that instead of instructing his patient to eat when feeling anxious, teaching him (her) how to relax via progressive muscle relaxation (PMR; Jacobson 1938) inhibited their anxiety. PMR involves the patient tensing different muscle groups in their body and then relaxing via deep breathing. Lastly, Wolpe would expose the patient to low-grade anxiety-producing situations, and the patient would practice PMR until their anxiety had reduced to 20 or lower. He would continue this process, gradually climbing up the hierarchy. Wolpe found systematic desensitization to work especially well when treating phobias, an extreme or irrational fear.

Wolpe believed that the principle of reciprocal inhibition could be applied to those who feel socially anxious, as well as those who feel angry. He was a pioneer of a technique called *assertiveness training* (Wolpe 1958). Similar to when he was treating those suffering from anxiety, assertiveness training involves counterconditioning the patient's angry or passive response with a friendly and affectionate response. Wolpe would have his patients practice the assertive response in the therapy session to replace the patient's passive or aggressive response.

Wolpe's work on systematic desensitization, assertiveness training, and applying PMR earned him the title "Father of Behavior Therapy." His work led to many other great findings, including exposure therapy (Telch et al. 2014). Exposure therapy is similar to systematic desensitization, in that the patient is exposed to fearful stimuli;

however, the fundamental premise is different. Systematic desensitization is based on the principle of reciprocal inhibition (Wolpe 1958), whereas exposure therapy is based on habituation (cf. Schare and Itzkowitz 2017). Systematic desensitization attempts to gradually replace an anxious behavior with a relaxing behavior. Exposure therapy immerses the patient in a highly anxiety-producing situation, and the anxiety-provoking stimulus is repeatedly presented until the patient's arousal level begins to decrease. A key component of exposure therapy is preventing escape (leaving an anxiety-producing situation) and avoidance (not engaging in anxiety-producing situations). Escape and avoidance both work against habituation and only increase the association between the stimulus and anxiety and the patient's response. Exposure therapy is just as effective as systematic desensitization and requires considerably less time in treatment. Habituation is likely to occur at a faster rate if the stimulus is high intensity and presented frequently. Exposure therapy is used to treat anxiety disorders, obsessive-compulsive disorder (OCD), and posttraumatic stress disorder (PTSD).

Exposure therapy can be conducted one of three ways: imaginal, in vivo, or virtual reality (VR). Imaginal exposure therapy involves having the patient visualize the anxiety-provoking stimulus. The benefits of imaginal exposure are that it does not require any additional resources on the part of the therapist and the therapist controls the stimulus. In vivo exposure involves presenting the patient with the real anxiety-provoking stimulus (e.g., spider, heights, social rejection). The drawback of in vivo exposure is the therapist's lack of control over the environment. The therapist has more control over creating an imaginal stimulus as opposed to presenting an in vivo stimulus. VR exposure is relatively new and provides an alternative to imaginal and in vivo exposure (Parsons and Rizzo 2008). In VR exposure, the patient is presented with a virtual creation of the target stimuli. The therapist has control over what stimuli are presented (contrary to in vivo exposure), and it is one dimension closer to resembling a real stimulus compared to imaginal exposure. Current research is inconclusive as to which approach

is most effective, though all three approaches are validated (cf. Telch et al. 2014; Parsons and Rizzo 2008).

Pavlov's work on classical conditioning has been very influential in explaining how learning occurs through associations and has led to the abovementioned therapeutic techniques. It has helped not only explain, control, and predict behavior but also replace maladaptive behaviors with more functional behaviors. However, it cannot explain how all behaviors are learned, and as such, researchers continued to look for other explanations.

## Neobehaviorism

### Methodological Behaviorism and Radical Behaviorism

While scientific method legitimized psychological research and gave merit to the field, observable behavior alone cannot account for the entirety of an organism's experience. *Radical behaviorism* posits that there is merit to considering the private mental activity of an organism (such as thoughts and feelings), along with biological factors and genetic factors. Yet, radical behaviorists do not believe that private experiences are a cause of behavior. Radical behaviorists seek to demonstrate connections between behavior and environment and are focused less on causation due to thoughts and feelings (Baum 2011).

Early insights that contributed to the philosophy of radical behaviorism were provided by early psychologist *Edward Lee Thorndike* in the late nineteenth century. Thorndike aimed to investigate animal intelligence. He confined a cat inside a puzzle box that contained various objects, some of which would open the box and encouraged the cat to escape confinement by placing a scrap of fish outside the box. Thorndike took care to record the specifics of his experiments, from the dimensions of the boxes to the ages of the thirteen cats he used as subjects (Thorndike 1927). This showed an experimental design that diverted from the common case study approach that was popularized in psychology at the time and several years before Watson introduced the Behaviorist Manifesto.

Thorndike's experiment could be replicated by any interested reader and featured multiple subjects (a group of cats instead of one individual cat). These studies reflected the scientific integrity and objectivity that Watson later promoted as a tenet of behaviorism.

Each cat was placed in the same puzzle box several times over. Thorndike observed that the first time the cats escaped, it was by trial and error. The cats would claw or bite objects until the door opened. Every time the cat was placed back in the box, they would escape faster than the previous time. The cats learned that manipulating certain objects led to a favorable outcome that freed them. Thus, Thorndike deduced that the cats learned how to open the box through successive trials. Thorndike termed his resulting theory the "law of effect," which stated that when a behavior has a satisfying consequence, the behavior would be more likely to be repeated and when the response is unpleasant, the behavior would be less likely to be repeated. Thorndike viewed the cats as being "pleased" by escaping the box and attaining the fish, which caused them to escape the box quicker (Thorndike 1927). From Thorndike's foundations and theory of behavior came a new model of operational behavior or behavior that operates on the environment the way that the cats manipulated objects to leave the boxes.

### Skinner's Operant Conditioning

The model of operant conditioning that Thorndike conceptualized was later actualized by B.F. Skinner. Skinner was an inventive, studious man who attended college intending to study writing. Yet, he left graduate school in the pursuit of psychology because he had "nothing important to say" as a writer (Skinner 1967). His research built upon the findings of Thorndike and Pavlov, and yet, Skinner moved away from their ideologies in his own conceptualization of behavior. Skinner believed that Thorndike's references to mental states using the term "pleasure" was an inaccurate label to use when it came to studying behavior. In addition, Skinner (1938) did not completely believe that Pavlov's (1927) work on reflexive behavior accounted for all learning. For example, a student may tremble at the sight of their teacher

carrying a large stack of exam papers into the classroom. Yet, classical conditioning cannot account for why the same student studied every day for an entire week leading up to the exam. Skinner's resulting conclusion was that there must be another way to learn behavior, because not every behavior is reflexive. He referred to these other behaviors as being "emitted" by an organism and explained these emitted behaviors through operant conditioning.

*Operant conditioning*, or instrumental learning, was defined by Skinner as behavior that occurs because it was previously instrumental in producing certain consequences (Skinner 1938). It is a behavior that changes consequences in an organism's environment. For example, it is a logical assumption that the student studied every day for their exam so that he would receive an impressive grade on the exam. This student may have learned that when he operates in a certain way and carry out a certain behavior (in this case, studying), his grades improve. A grade is an outcome that makes the student study more, and by studying, the student "operates" upon their environment. Or, perhaps this same student did not study for a previous test in this same class and they received a poor grade. The student's studying behavior could also be a way to avoid an unfavorable grade. The student's studying behavior is instrumental in establishing the outcome. This led to Skinner's development of the "Law of Effect – Reinforcement," where he identified that behavior that is reinforced will repeat and is "strengthened" and that behavior that is not reinforced will extinguish or "weaken" (Skinner 1938).

To study the ways that organisms operate upon their environments, Skinner created boxes similar to Thorndike's, referred to as "Skinner boxes." An animal, such as a rat, would be free to move around the box. A lever in the box, when pressed, would deposit water or a food pellet. The rat would press the bar and receive the reward and having been reinforced for pressing the lever would be more likely to press the bar with greater frequency. The *rate* of the response increased due to the rat being positively reinforced. The *operant response*, in this case the lever press, has a

positive effect on the environment and will be more likely to be repeated (Skinner 1938).

## Contexts of Operant Conditioning

### Reinforcement

Skinner (1938) identified that there were three types of responses that could follow behavior: neutral, positive, and negative. A neutral operant is a response from the environment that does not increase or decrease the amount of times that a behavior is repeated. Reinforcement is a response that increases a behavior and can be either positive or negative. It is important to note that the terms "positive" and "negative" are used to refer to "addition" and "subtraction," respectively. They are not supposed to signify something that is "good" or "bad."

*Positive reinforcement* is when a behavior is strengthened through the addition of a rewarding stimulus (Skinner 1938). Imagine that when a child makes his bed, he receives \$10 from their parents. He is positively reinforced (\$10) for his behavior (making the bed), which will make him more likely to make his bed in the future. Or let's consider the student who studied for his test because they received a good grade when he studied in the past. The good grade is the reinforcer, and the behavior is studying. Skinner praised positive reinforcement as the most effective way to reinforce a behavior.

*Negative reinforcement* is when a behavior is strengthened through the removal of an aversive or noxious stimulus. A negatively reinforced behavior allows the animal to escape from an unpleasant stimulus/consequence (Skinner 1953). There are two specific types of negative reinforcement: escape and avoidance. *Escape* is when an animal attempts to alleviate an aversive stimulus by leaving an unpleasant condition. An example of this is when someone takes an aspirin to alleviate a headache. Taking aspirin removes the aversive headache, so the behavior is negatively reinforced. On the other hand, *avoidance* is when an animal engages in a behavior to prevent the presence of an aversive stimulus. Putting on sunscreen before a day at the beach is a behavior to avoid a future negative consequence (sunburn).

Reinforcers can also be “primary” or “secondary.” A *primary reinforcer* is a reinforcer that is satisfying on its own without being linked to another reinforcer. This can include food, water, sleep, shelter, touch, or feelings of pleasure. All of these examples have innate reinforcing qualities to organisms. A *secondary reinforcer* (also referred to as a conditioned reinforcer) has no innate reinforcing value until it is linked with a primary reinforcer – one example is money. Green pieces of paper are not innately reinforcing to humans. Yet, humans learn that money can be used to acquire primary reinforcers (e.g., food, water, shelter). This paired association is what makes money reinforcing.

### Punishment

Reinforcement is a stimulus that increases the likelihood of a behavior, while punishment is a stimulus that decreases the likelihood of a behavior. The term “punishment” does not have any connotation of “good” or “bad” in behaviorism. Instead, it simply indicates a decrease in a response. There can also be positive and negative types of punishment, like positive and negative reinforcement.

*Positive punishment* is when an unpleasant stimulus is introduced to decrease or weaken a behavior (Skinner 1953). A classic example of positive punishment is corporal punishment. Perhaps a parent hits a child after the child steals from the cookie jar before dinner. The unpleasant consequence (hitting) will decrease the undesired behavior in the future (stealing cookies). However, in behaviorism, the term “punishment” does not always indicate a penalty. Another example of a punisher is when the child leaned on the counter to get into the cookie jar, and rested their hand on the hot stove in the process. The introduction of an unpleasant consequence (a burned hand) will decrease the likelihood that the child will engage in the behavior (touching the stove to get the cookie jar) in the future. Thus, the cookie-stealing behavior is weakened.

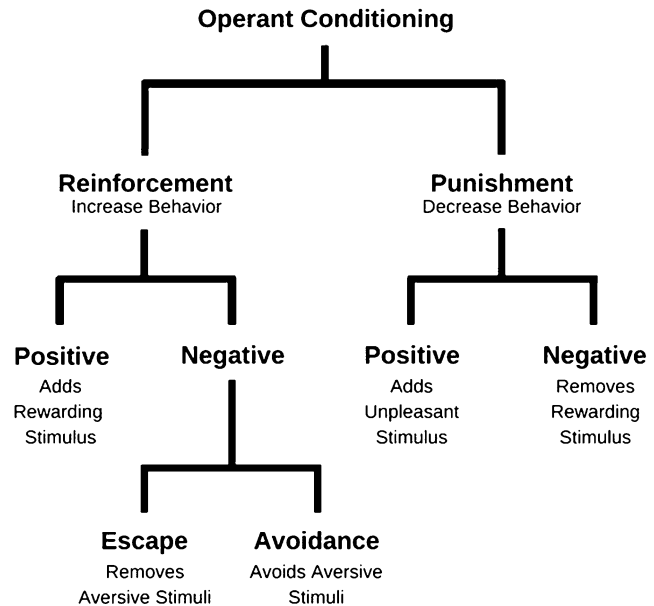
*Negative punishment* is when a favorable stimulus is removed after a behavior occurs, to decrease or weaken the behavior (Skinner 1953). One common example of negative punishment is

when a student breaks the rules and receives detention. The student is removed from a favorable environment (leaving school on time to go home) in order to decrease their rule-breaking behavior. Another example of this is placing children in time-outs or when a parent takes away cellphone/computer/TV usage. There is no noxious consequence added, but there is something positive taken away, and this removal of the positive consequence will cause a reduction of the undesired behavior (see Fig. 2).

**The Case against Punishment** Skinner spoke out against all uses of punishment and stated that they were ineffective compared to reinforcement. He expressed that while punishment is the most common type of behavioral control used in the world, that punishment would only temporarily “suppress” a behavior and that it could create other unwanted consequences (e.g., fear and aggression; Skinner 1953). There is some sound logic in Skinner’s claims. When an animal is punished, a response is decreased, but, if a desired target behavior is never increased, the animal will not have any other response to the stimulus. Punishment *does not* promote learning. It is commonly accepted that when an undesired behavior is decreased, a desirable target behavior should be increased as well. If a teacher ignores a child every time the child speaks without raising her hand, the teacher should call on the child when she raises her hand appropriately (and can even compliment the child, as well).

Instead of punishment, Skinner believed in extinguishing behaviors through nonreinforcement and spoke out widely against the use of punishment to control behavior. Research was conducted in a laboratory on the same floor as Skinner’s office by Tom Azrin who attempted to undermine Skinner’s poor view of punishment. Overall, Azrin and his colleague Holz (Azrin and Holz 1966) determined that punishment is uniquely effective compared to other forms of behavioral suppression. When performed correctly, punishment is just as effective in extinguishing behavior as extinction. Punishment operates on a different schedule of effectiveness compared to reinforcement. Continuous punishment produces the

**Behaviorism,**  
**Fig. 2** Operant  
conditioning



greatest reduction of behavior, rather than an intermittent schedule of punishment. A sudden introduction of an immediate and intense novel punishment is the most effective way to use punishment to reduce behavior.

There are times that punishment has an appropriate place in behavioral reduction. Lang and Melamed (1969) treated a 9-month-old infant who was regularly regurgitating his food. The infant was at risk of death due to starvation. The only solution that worked after multiple failed medical interventions was to provide a brief, painful shock to the infant's leg every time he began to regurgitate. This is an example of an ethical use of positive punishment. This life-saving punishment procedure reduced the undesirable behavior faster than extinction would have.

#### Schedules of Reinforcement

Behavior is rarely *continuously* reinforced; more often, animals are reinforced *intermittently*, meaning that reinforcement is not always consistently contingent upon the introduction of a stimulus. For example, a cat that prowls the streets for a good meal might not catch a mouse every time he goes out hunting. Yet, the cat does not stop hunting, as the cat has been reinforced for it. It is important to understand the *schedule of*

*reinforcement* or the schedule that determines how often a reinforcer is delivered after a behavior. These schedules affect the ways that an animal learns a response and then how the response is maintained over time (Ferster and Skinner 1957).

Continuous reinforcement is most effective when first beginning to teach a response. To teach a dog to sit on command, the most effective method is to reward the dog for sitting every time she hears the word "sit." Two paradigms define intermittent schedules of reinforcement: *fixed* or *variable* and *interval* or *ratio*. Fixed reinforcement refers to a set number of responses or length of time between reinforcements. Variable refers to when the number of responses or length of time varies. Intermittent reinforcement can also be delivered on an *interval* or *ratio* basis. Interval means that the schedule is based on the amount of *time* that passes between the reinforcements. Ratio means that the schedule is based on the *number of responses* between reinforcements. Thus, there are four different types of intermittent reinforcements. These are listed in order from the "weakest" to "strongest" (Ferster and Skinner 1957).

A *fixed-interval schedule* of reinforcement is when a behavior is rewarded after a set amount of time. A washing machine that always runs on a 45-min cycle operates on a fixed interval of

reinforcement. The individual doing laundry will be more likely to perform the reinforcing response (checking to see if the clothes are clean) closer to the end of the 45-min time frame, opposed to immediately after the laundry is loaded. There is a significant pause after reinforcement, where the individual will not perform the response until it comes time for reinforcement to occur again. This creates a “scallop-shaped” response (see Fig. 3).

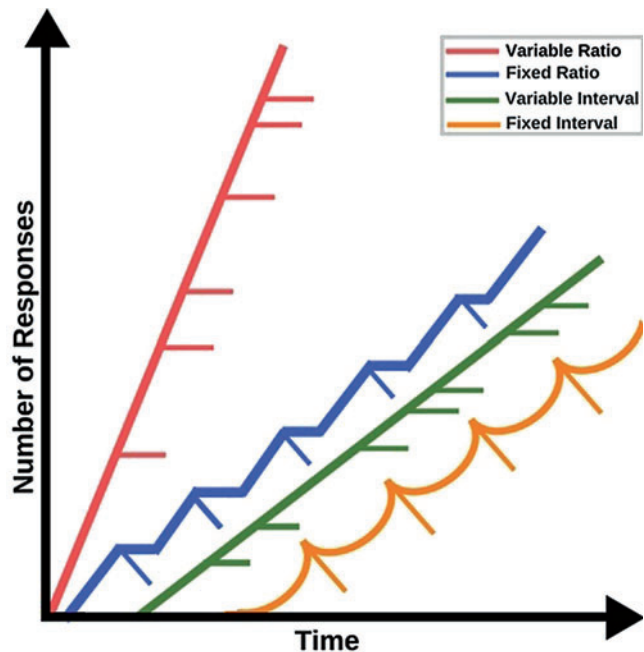
In a *variable-interval schedule*, a behavior is reinforced based on varied amounts of time. It is unpredictable, so an individual can never be sure when the reinforcement will be delivered. A professor may deliver pop quizzes on a variable-interval schedule by giving the quizzes at unpredictable times. During 1 week of class, students may take two quizzes. On other weeks, there may be no quiz at all. This reinforces students to study because they will not know when they will have a pop quiz. The rate of responding in a variable-interval schedule is moderate but constant. The students will likely not study the way they would for a large exam the next day. There is typically very little pause after reinforcement is given.

A *fixed-ratio schedule* means that reinforcement is delivered after a certain number of

responses. A student earns allowance from her parents for every five homework assignments that she completes. Fixed-ratio schedules promote quantity of response, meaning this student will be likely to do her homework every single night. However, she may not work hard and receive a failing grade on all of them, because the quality of her response is not promoted. A fixed-ratio schedule results in a high, consistent response rate until the reinforcement is delivered. After the reinforcer is administered, there will be a pause in responses before responding resumes.

In a *variable-ratio schedule*, the reinforcement is delivered after a varied number of responses. This schedule creates the highest and most consistent rate of responding of any of the reinforcement schedules. The animal cannot predict when the reinforcer will be delivered. An example of this is the way that slot machines operate. A slot machine operates on an unpredictable win schedule, but players know that eventually there will be a payout because there is a constant probability of hitting the jackpot. Players hesitate to stop playing at the machine even after continual losses due to the possibility that the next game will be a winner.

**Behaviorism,**  
**Fig. 3** Schedules of  
reinforcement





## Extinction

Of course, an individual would not sit at a slot machine forever on the expectation of winning if there was never any reward. In Skinner's autobiography, he told the story of how he discovered extinction in the operant conditioning paradigm. Though much of Skinner's experiments were performed with intention, he found extinction through an accident in his laboratory. A rat was in a Skinner box, pressing a lever for food pellets when the pellet dispenser broke. The rat continued to press the lever for pellets, but no pellets came (thus, the rat was not reinforced for pressing the lever). Soon, the rat stopped pressing the bar in the same way that Pavlov's dogs stopped salivating to the sound of a metronome when no food was delivered (Pavlov 1927; Skinner 1979). Both responses, the lever-press and the salivation response, were extinguished through *extinction*. Extinction is when a behavior is no longer reinforced (the lever-press stopped delivering pellets), and so the response decreases until it stops (the rat stopped pressing the lever; Skinner 1938).

When a behavior no longer leads to reinforcement, there is sometimes an increase in the target behavior before there is a decrease. This is referred to as an *extinction burst*. There may be new behaviors that accompany the increase behavior. A child throwing a tantrum in the store may scream louder or drop to the floor and roll around, all behaviors in escalation of their original tantrum behavior. The extinction burst serves a behavioral purpose. A behavior that has previously produced rewarding consequences might still have a chance of producing a rewarding consequence.

## Differential Reinforcement

To increase target behaviors while decreasing other target behaviors, simple schedules of reinforcement and extinction are used together in differential reinforcement procedures. *Differential reinforcement of alternative behavior (DRA)* decreases an undesirable behavior through extinction (or, less commonly through punishment) while reinforcing an alternative response (Miltenberger 2008). An example of DRA is when a parent

ignores their screaming child and only responds when the child uses calm coherent words.

*Differential reinforcement of other behavior (DRO)* is also referred to as "omission training." This is when a positive reinforcer is only delivered (and delivered periodically) when a subject engages in something besides a target response (Miltenberger 2008). A child with a nail-biting habit can be reinforced when he does anything with his hands besides biting his nails, such as clapping or keeping his hands in their lap.

*Differential reinforcement of incompatible behavior (DRI)* decreases an undesirable behavior through introducing a competing behavior. Both behaviors cannot occur at the same time, and the competing behavior is reinforced instead of the undesirable behavior (Miltenberger 2008). Owners who are teaching their dog not to jump on guests should have the guests ignore the dog when it jumps on them. When all four of the dog's feet are on the ground near a guest, he can be provided with reinforcing pats on the head or treats. The dog cannot engage in the jumping behavior and the standing behavior at the same time.

## Shaping and Chaining

Many individuals who are handicapped rely on a service dog for assistance. The dog may perform tasks that the person is not mobile enough to complete without help, such as loading the laundry machine. But, a dog does not understand how to do laundry nor can a dog comprehend verbose instructions. Likewise, the process of loading a laundry machine is far more complicated than a simple command (such as "sit" or "stay"). The seemingly monumental task of teaching a service dog can be approached through *shaping*. Shaping is defined as differential reinforcement of "successive approximations" that will eventually lead to the full response (Skinner 1953). At first, the dog may be reinforced every time he looks at a sock. Then, he will be reinforced any time he looks at a sock and also steps toward it. The dog should no longer be reinforced for simply looking at the sock. Through the use of shaping these successive approximations, the dog will eventually be able to pick up the sock.

Another reinforcement technique that may need to be used for this dog is *chaining* or the process of linking behaviors together so that the result of each behavior becomes the stimuli for the next behavior (Skinner 1934). The dog may be taught to pick up the sock and then bring the sock near the laundry machine. Once the dog has successfully picked up the sock and brought it to the machine (the first and second behaviors in the chain), the dog can be taught to drop the sock into the laundry machine. The desired behavior can be taught as an entire series with specific prompts for each step in the chain (e.g., the dog picks up the sock with its mouth, walks to the washer machine, stands up on his hind legs, opens his mouth, and drops the sock into the washer machine).

### Applied Behavior Analysis

Skinner boxes are an effective way to reinforce one rat at a time, yet the external world does not tend to isolate an individual for behavioral observation. The principles of Skinnerian behaviorism and radical behaviorism serve as the foundation to the field of *applied behavior analysis (ABA)*. The difference between ABA and operant conditioning exists in examining the function of a behavior in the environment and developing systemic interventions to modify behavior. The first “A,” *applied*, is a focus placed on the social significance of the behavior, taking the behavior out of a “box” and placing it into the environment. The behavior must be observable for objective measurement. The last “A,” *analysis*, indicates that behavior must be measured in ways that demonstrate the impact of the environment. An effective behavior analyst should have an understanding of the environmental settings that make an organism engage in a behavior (Baer et al. 1968).

Success has been gained through the use of the principles of applied behavior analysis in reinforcing target behaviors in a larger population. Specifically, *token economies* can reinforce specific target behaviors on a large scale with many individuals in a system (such as students in a school or inmates in a prison). Tokens are provided as a secondary reinforcer and can be exchanged for desirable items. These may be tallied

as points, kept on a chart, or distributed as physical currency. The tokens are provided when a desired target behavior is performed and can be distributed by teachers or correctional officers. For example, tokens can be administered at a school when a student clears their tray at lunch. Other students will be motivated when they see the first student earn a reward. The tokens can be exchanged in a “store” for backup reinforcers, such as toys, food, or passes for leisure time (items that “back up” the tokens and give the tokens value). Token economies are effective in increasing target behaviors when the tokens are provided consistently and immediately in response to a target behavior. Though token economies are not transferable out of a closed system into the open world, they can effectively target and change behavior within the system.

### Skinner’s Philosophy of Behaviorism

It is important to note that many individuals view radical behaviorism as a means to predict all behavior of all organisms. This suggests that organisms do not have any true free will and that all sequences of behavior are inevitable. The philosophy that all behaviors are predetermined is referred to as *determinism*. Skinner openly stated that he believed free will to be an illusion, because operant conditioning suggests that consequences are predictable. An organism will engage in specific behaviors depending on the environment in which the organism exists (Skinner 1974). Skinner also stated that it would be nearly impossible to map out every behavior in which an organism would ever engage (Skinner 1938). Since it is impossible to identify all the variables determining a target behavior, the adoption of a fully deterministic approach can appear extreme. Yet, one can still support determinism while understanding that it is impossible to know all the predictor variables and their value to the organism.

Skinner believed that there was a definition of freedom that was still in line with the deterministic approach. He argued that empowering individuals was a useful tool to incite rebellion against oppressive political authorities. Yet, he pointed out how these overcontrolling authorities were

only in power due to the government that humans built. The freedom that Skinner supported was to submit to the forms of control that are the most scientifically effective, opposed to maintaining a façade of autonomy under self-imposed political oppression. Along with reshaping freedom, Skinner rejected the notion of dignity or the idea that individuals deserve credit or punishment for their behaviors. He suggested that society does not provide credit to those who behave under duress or control and that there are forces in control of all individuals (Skinner 1971). In this view, individuals do not act creatively upon their environments and should not be rewarded as if they do.

The publication of Skinner's novel *Walden Two* (Skinner 1948) brought his idealistic sociopolitical worldview into prose in a fictional utopia founded on behaviorism. He spoke of learning incentives that could contribute to human happiness while reducing systemic injustice and power imbalances. The fictional society Walden Two is built on a program of behavioral engineering that began at birth for all members that makes individuals motivated and cooperative. Man is assumed to not be autonomous. There is a community-based governance that is modified with empirical evidence at the heart of Walden Two, with no governing body. Individuals engage in work simply because they enjoy contributing to the community. Personal expressions of gratitude toward other individuals are outlawed, as this supports the idea of dignity. Skinner described the citizens of Walden Two as harmonious and happy, though only provided a foggy description of how their daily lives functioned. He gave no discussion on how interpersonal conflict or differences could be resolved. Nonetheless, the theoretical society gave Skinner a platform to put his behaviorism into a context where a system of reinforcement could produce all of society's advances.

## Sociobehaviorism

Despite Skinner's beliefs, not everyone believed reinforcement and associations could account for all learning. Albert Bandura, a professor at

Stanford, is most recognized for proposing how social interactions lead people to learn new information. He believed learning could occur through *modeling* (aka *observational learning*), watching someone else perform the behavior (Bandura 1986). Bandura posited that most learning is achieved through modeling, and at times learning can only be achieved through modeling. A medical student does not learn about surgical procedures by practicing on patients but instead watches an accomplished surgeon perform the procedure. Bandura expanded his work into a theory known as *social learning theory*, which became the cornerstone of sociobehaviorism.

There are three tenets of social learning theory: (1) People learn through observations (modeling). (2) Internal mental states are an integral component of observational learning. (3) A new behavior can be learned, but it does not mean the person will perform the behavior. Bandura changed the name of social learning theory to *social cognitive theory* to stress the importance of internal mental states, deviating from typical behaviorist ideals.

## Reciprocal Determinism

Social cognitive theory proposes a *continuous, dynamic* relationship with personal factors, environmental factors, and behavior, known as *reciprocal determinism* (Bandura 1986). These three factors do not equally influence behavior, but rather the factors' influence varies based on context. Personal factors include cognition (e.g., expectations and self-judgments), self-efficacy, motivation, and personality. As stated above, Watson and Skinner did not account for these factors. Bandura believed self-efficacy greatly impacts behavior as individuals with higher self-efficacy, the degree to which an individual can master a skill, are more likely to have confidence in their abilities and thus behave differently than those with low self-efficacy. When an individual believes a behavior will be effective, their motivation to perform the behavior increases. If the behavior *is* effective, the individual may be rewarded through *intrinsic reinforcement* (e.g., pride, satisfaction, sense of accomplishment) or if the behavior is ineffective, the individual may

be punished through *intrinsic punishment* (e.g., disappointment, shame, guilt).

Environmental factors include the situation, models, relationship to the models, roles, as well as reinforcers and punishers. As discussed above, the environment may reinforce or punish a behavior, which is likely to impact the behavior re-occurring. A model demonstrates how to perform the behavior. The model and the individual's relationship to the model can alter how quickly the individual learns the behavior. Placing importance on self-efficacy, Bandura believed that the environment should improve self-efficacy to motivate the individual to perform the behavior.

The third factor is behavior, and it includes knowledge, complexity, duration, and skill of the behavior. The knowledge of the individual and the complexity of the task influence the motivation of the individual to perform the behavior. In addition, the individual's skill level influences how well the individual thinks he will perform on the task, which relate to low self-efficacy. When an individual has low self-efficacy, he is less likely to perform the behavior.

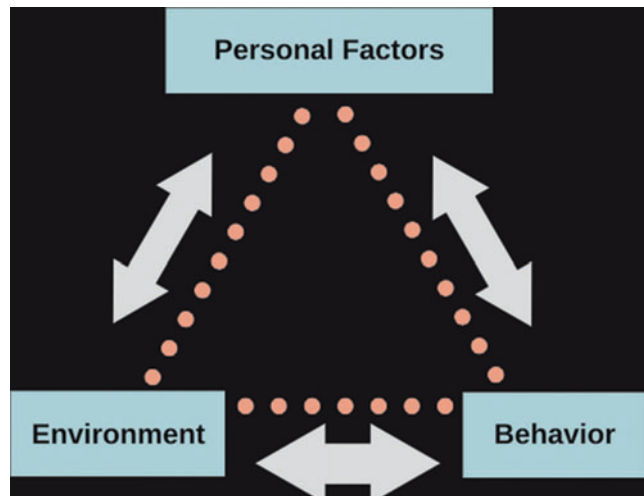
As mentioned above, Bandura believed that all three of these factors (personal, environmental, and behavior) influences behavior. An example of how all three factors influence one another is when a father teaches his son how to hit a baseball. The son first watches the father (model) swing the bat (environmental factor). The son then

thinks he is able to swing the bat the same way (personal factor) and models his father's behavior (behavior). The father then rewards his son by saying "good job" (environmental factor). This increases the son's self-efficacy (personal factor), which means the son is more motivated and thus more likely to believe he can swing the bat, increasing this behavior (behavior) (Fig. 4).

### Observational Learning

As seen in Bandura's concept of reciprocal determinism, social interactions influence behavior. Bandura emphasized how observing another perform a behavior can lead to a change in behavior. He first noticed this in his classic studies known as the *Bobo doll experiments* (Bandura 1965; Bandura et al. 1961, 1963). He had children watch adults either aggress (verbally and physically) on or ignore a clown toy called a Bobo doll. The children who saw the adults act aggressively were more likely to aggress (verbally and physically) on the Bobo doll. Bandura found that while watching the adults aggress was important, the sexes of the adults and children played a role as well. The boys watching adult males physically aggress on the Bobo doll were the most likely participants to imitate physical aggression. Interestingly, Bandura found that girls who witnessed adult females verbally aggress on the Bobo doll were most likely to imitate verbal aggression (Bandura et al. 1961). This led Bandura to

**Behaviorism,**  
**Fig. 4** Reciprocal  
determinism



conclude that humans learn through observations and that the characteristics of the model are also important.

The second Bobo doll experiment reemphasized that a model's characteristics are important (Bandura et al. 1963). Bandura stated that there are three basic models of observational learning: live, verbal instructions, and symbolic model. Live observational learning is watching the model perform the behavior in vivo. Verbal instructions are when the observer reads a description of the behavior. Symbolic models are real or fictional characters performing a behavior in other forms of media (e.g., books, movies, television programs).

Bandura (1965) built on the previous Bobo doll studies by examining how children reacted when they watched a video of a model aggress on the Bobo doll and the model was either reinforced (given candy), punished with the warning, "don't do it again," or experienced no consequences. Bandura found that children who were shown a video where the physical aggressor was punished were less likely to be aggressive. The next phase of the study asked the children to imitate the behavior they saw on the video. The children were able to accurately imitate the behavior, showing that reward and punishment do not influence retaining information, but rather, only if the behavior is demonstrated. This is a core concept of social cognitive theory, emphasizing how a behavior can be learned but not performed due to the individual's lack of motivation, not lack of knowledge.

There are four steps the observer must engage in for the model to effectively transmit the information: attention, retention, reproduction, and motivation (Bandura 1986). The observer must pay *attention* to the model to process the information. There are several factors that influence attention: accessibility, relevance and complexity of the task, functional value of the behavior, as well as the observer's characteristics – cognitive capability, values, preconceptions, emotional arousal, and self-efficacy. In addition, accessibility is influenced by how much the observer identifies with the model and the observer's expectations of the behavior. *Retention* is the observer's ability to

remember how the behavior was performed, as well as the result of the behavior (i.e., reinforced, punished, or neutral). It may involve the individual mentally reenacting the behavior. The third step is physically *reproducing* the behavior so that it leads to skill advancement and improvement. This step may also include feedback from individuals, including the model. The last step is *motivation*. The observer learns the skill by the reproduction phase but must be motivated to perform the behavior. Two factors that affect motivation are vicarious reinforcement and intrinsic reinforcement. If the observer sees the model reinforced for their behavior, the observer has increased motivation to perform the behavior. This is known as *vicarious reinforcement*. Even though the model was reinforced, vicarious reinforcement leads to a positive emotion for the observer as he is excited about the potential of receiving the reward. If vicarious reinforcement is not experienced, the observer may learn the behavior, but may not be motivated to perform it, relating back to the third concept of social cognitive theory mentioned above. Also mentioned above, motivation may increase based on intrinsic reinforcement (e.g., pride, satisfaction, sense of accomplishment), leading to the production of the behavior.

### **Outcome Expectations and Self-Efficacy**

After watching the model perform the behavior and seeing the result (i.e., reinforcement, punishment, or neutral), the individual begins to develop expectations of the outcome. The individual does not necessarily believe that the *same* reward or punishment may occur but recognizes that behavior is context dependent and instead a *similar* outcome will occur. *Outcome expectations* (Bandura 1986) are an individual's predictions about the functionality of a behavior and how the environment will respond to the behavior. Bandura believed that outcome expectations along with efficacy judgments are the *best predictors* of behavior. If an individual has high outcome expectations and efficacy judgments, he is more likely to engage in the behavior. *Efficacy judgments* (Bandura 1986) are the individual's appraisals of how well he can perform the specific



behavior. For example, a child learning to read may be reinforced for every sentence he reads correctly (outcome expectations). However, the child may not believe he can read even three words correctly (efficacy judgments) and, therefore, may not read. Generalized efficacy judgments directly relate to *locus of control*. Rotter (1966) explained locus of control as the extent to which one believes he has control over the situation. The spectrum of locus of control ranges from internal to external. An example of complete internal control is the individual believing that he has absolute control over the outcome. Complete external control is the individual believing that he has no control over the outcome.

These cognitions (outcome expectations, efficacy judgments, and locus of control) relate to self-efficacy (Bandura 1986). As mentioned above, self-efficacy is the individual's belief that he can master a skill. Self-efficacy affects how goals, tasks, and challenges are approached. If an individual believes he can perform the behavior well and produce a positive effect, he is more likely to behave. If the individual does not believe he can perform the behavior well and/or produce a negative effect, then he is less likely to engage in the behavior. Bandura found that individuals with high self-efficacy are more likely to model behaviors than individuals with low self-efficacy. He credited this finding to the belief that individuals with low self-efficacy believe they will not perform the task well and thus avoid the tasks.

Bandura (1986) believed that increasing an individual's self-efficacy could produce therapeutic effects, such as the individual having a more positive affect and produce more functional behaviors. Bandura presented three ways self-efficacy could be increased: mastery experience, social modeling, and improving physical and emotional states. *Mastery experience* has the individual focus on simple tasks that are easy to achieve, gradually increasing to more complex tasks. This increases the individual's efficacy judgments, which increases their motivation to perform the behavior. *Social modeling* is having the individual participate in observational learning. An individual with low self-efficacy can develop it by paying close attention to a model's behavior. Compared

to the individual with high self-efficacy, Bandura believed that the individual with low self-efficacy may need to watch the model perform the behavior more often. This is not because he does not retain the information but rather because he does not *believe* he retains the information and/or will not be effective. Bandura (1986) also emphasized *improving physical and emotional states*. An individual who is stressed is less likely to believe he can effectively perform a new behavior, compared to an individual who is rested.

Bandura's social cognitive theory is one of the first behavioral theory focusing on cognitions. He described how the environment, behavior, and the personal factors (e.g., cognitions) dynamically influence one another. He called into question Skinner's claim that reinforcement and punishment can account for all learning; instead, Bandura believed that observational learning accounted for more learning than operant conditioning did. Social cognitive theory's addition of cognitions addressed the growing disconnect of research showing thoughts can influence behavior.

## Conclusion

Behaviorism rose from rebellious beginnings as an alternative movement in a world of unobservable psychology. With the rise of behaviorism, mentalistic approaches toward patients became outdated. However, the latter half of the 1900s marked a time for psychology to change again, with a new focus on the importance of cognition. Noam Chomsky, a linguist, philosopher, and cognitive scientist, wrote a review of Skinner's work that served as a call to arms. Chomsky did not deny the points that Skinner made but argued for the importance of examining higher mental states. Specifically, Chomsky believed that language acquisition could not be explained through traditional behaviorist belief (Chomsky 1959). Thus, the cognitive revolution began, though behaviorism was not forgotten. As Bandura expressed through his social cognitive theory, the two could be blended effectively into a new paradigm. In 1986, Clark noticed that cognitive misinterpretations of physical sensations would cause patients



to catastrophize symptoms of anxiety (e.g., “I am having a heart attack”), causing panic attacks. He posited that there was merit to treating the cognition that maintained the behavior (Clark 1986). Thus, came the beginnings of cognitive behavioral therapy. Cognitive behavioral therapists hypothesize that the activating events lead to cognitions that then affect one’s behavior. These cognitions are treated as new stimuli and new responses in the stimulus and response chain. Behavior therapies placing an importance on thought and internal experiences created a well-rounded therapeutic orientation that allowed for patients to express their thoughts and feelings while also implementing behavioral change (Rachman 2009).

Modern therapeutic application of behaviorism calls for clinicians and patients to work together in addressing, and ultimately changing, behaviors that interfere with the patient’s functioning. The tenets set forth in Watson’s writings transformed psychology into a science. Behaviorism values observation over assumption in research and behavioral change over mentalistic introspection in therapeutic practice. New waves of behavior therapies are created, researched, implemented, and popularized in cycles. Yet, they all build off the foundational underpinnings that were laid out by the forerunners of behaviorism.

## Cross-References

- ▶ Aristotle
- ▶ Associative Learning
- ▶ B.F. Skinner
- ▶ Classical Conditioning
- ▶ Cognitive Imitation
- ▶ Conditioned Response
- ▶ Conditioned Stimulus
- ▶ Counterconditioning
- ▶ David Hume
- ▶ Differential Reinforcement
- ▶ Edward Thorndike
- ▶ Extinction in Learning
- ▶ Free Operant Responses
- ▶ Generalization
- ▶ Higher-Order Conditioning
- ▶ Instrumental Learning
- ▶ Law of Effect
- ▶ Learning
- ▶ Negative Reinforcement
- ▶ Operant Conditioning
- ▶ Positive Reinforcement
- ▶ Reinforcement
- ▶ Social Learning
- ▶ Spontaneous Recovery
- ▶ Unconditioned Response
- ▶ Unconditioned Stimulus
- ▶ Vicarious Reinforcement

## References

- Azrin, N. H., & Holz, W. C. (1966). Punishment. In W. K. Honig (Ed.), *Operant behavior: Areas of research and application*. New York: Appleton-Century-Crofts.
- Baer, D. M., Wolf, M. M., & Risley, T. R. (1968). Some current dimensions of applied behavior analysis. *Journal of Applied Behavior Analysis*, 1(1), 91–97.
- Bandura, A. (1965). Influence of models’ reinforcement contingencies on the acquisition of imitative responses. *Journal of Personality and Social Psychology*, 1(6), 589–595.
- Bandura, A. (1986). *Social foundations of thought and action: A social cognitive theory*. Englewood Cliffs: Prentice-Hall.
- Bandura, A., Ross, D., & Ross, S. A. (1961). Transmission of aggression through the imitation of aggressive models. *Journal of Abnormal and Social Psychology*, 63(3), 575–582.
- Bandura, A., Ross, D., & Ross, S. A. (1963). Imitation of film-mediated aggressive models. *Journal of Abnormal and Social Psychology*, 66(1), 3–11.
- Baum, W. M. (2011). What is radical behaviorism? A review of Jay Moore’s conceptual foundations of radical behaviorism. *Journal of the Experimental Analysis of Behavior*, 95(1), 119–126.
- Clark, D. M. (1986). A cognitive approach to panic. *Behavior Research and Therapy*, 24(4), 451–470.
- Chomsky, N. (1959). A review of B.F. Skinner’s verbal behavior. *Language*, 35(1), 25–58.
- Ferster, C. B., & Skinner, B. F. (1957). *Schedules of reinforcement*. East Norwalk: Appleton-Century Crofts.
- Hume, D. (1740/2012). *A treatise of human nature* [E-reader Version]. Retrieved from <https://www.gutenberg.org/files/4705/4705-h/4705-h.htm>
- Jacobson, E. (1938). *Progressive relaxation*. Chicago: University of Chicago Press.
- Jones, M. C. (1924). The elimination of children’s fears. *The Journal of Experimental Psychology*, 7(5), 382–390.

- Lang, P. J., & Melamed, B. G. (1969). Case report: Avoidance conditioning therapy of an infant with chronic ruminative vomiting. *Journal of Abnormal Psychology*, 74, 1–8.
- Miltenberger, R. G. (2008). *Behavior modification: Principles and procedures*. Belmont: Thomson Wadsworth.
- Parsons, T. D., & Rizzo, A. A. (2008). Affective outcomes of virtual reality exposure therapy for anxiety and specific phobias: A meta-analysis. *Journal of Behavior Therapy and Experimental Psychiatry*, 39(3), 250–261.
- Pavlov, I. P. (1927). *Conditioned reflexes: An investigation of the physiological activity of the cerebral cortex*. Oxford, England: Oxford University Press.
- Pavlov, I. P. (1928). *Lectures on conditioned reflexes: Twenty-five years of objective study of the higher nervous activity (behaviour) of animals*. New York: Liverwright Publishing Corporation.
- Rachman, S. (2009). Psychological treatment of anxiety: The evolution of behavior therapy and cognitive behavior therapy. *Annual Review of Clinical Psychology*, 5, 97–119.
- Rotter, J. B. (1966). Generalized expectancies for internal versus external control of reinforcement. *Psychological Monographs: General and Applied*, 80(1), 1–28.
- Schare, M. L., & Itzkowitz, M. J. (2017). Habituation & exposure. In A. Wenzel (Ed.), *The SAGE encyclopedia of abnormal and clinical psychology*. New York: SAGE.
- Schultz, D. P., & Schultz, S. E. (2016). *A history of modern psychology* (11th ed.). Boston: Cengage Learning.
- Skinner, B. F. (1934). The extinction of chained reflexes. *Proceedings of the National Academy of Sciences of the United States of America*, 20, 234–237.
- Skinner, B. F. (1938). *The behavior of organisms: An experimental analysis*. New York/London: D. Appleton-Century Company, Incorporated.
- Skinner, B. F. (1948). *Walden two*. New York: Macmillan.
- Skinner, B. F. (1953). *Science and human behavior*. New York: Macmillan.
- Skinner, B. F. (1967). B.F. Skinner. In E. G. Boring & G. Lindzey (Eds.), *A history of psychology in autobiography*. Appleton-Century-Crofts: New York.
- Skinner, B. F. (1971). *Beyond freedom and dignity*. New York: Knopf.
- Skinner, B. F. (1974). *About behaviorism*. New York: Knopf.
- Skinner, B. F. (1979). *The shaping of a behaviorist: Part two of an autobiography*. New York: Knopf.
- Telch, M. J., Cobb, A. R., & Lancaster, C. L. (2014). Exposure therapy. In P. Emmelkamp & T. Ehring (Eds.), *The Wiley handbook of anxiety disorders* (pp. 717–756). Hoboken: Wiley.
- Thorndike, E. L. (1927). The law of effect. *The American Journal of Psychology*, 39, 212–222. doi:10.2307/1415413.
- Watson, J. B. (1913). Psychology as the behaviorist views it. *Psychological Review*, 20(2), 158–177.
- Watson, J. B., & Rayner, R. (1920). Conditioned emotional reactions. *Journal of Experimental Psychology*, 3(1), 1–14. <http://psychclassics.yorku.ca/Watson/emotion.htm>.
- Wolpe, J. (1958). *Psychotherapy by reciprocal inhibition*. Stanford: Stanford University Press.

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## Behavior Systems

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### Beginnings in Ethology

Nikolaas Tinbergen (1942) began to speak in terms of systems of behavior in his first manifesto of ethology. As there are systems of respiration and systems of digestion, for instance, in which multiple chores are accomplished in coordination by different parts to perform a complex function, there can be said to be systems of behavior that collectively accomplish complex chores such as feeding, finding mates, avoiding pain, and perhaps less obvious functions as well, such as play, grooming, or sociality. Tinbergen (1942) stressed that behavior has an organization and that this organization is hierarchical (Fig. 1).

### Behavioral Context of Behavior

At the core of a behavior systems approach is concern for how the various behavioral propensities of an animal's repertoire interrelate. Feeding, for instance, requires the unfolding of a complex sequence of behaviors. Focus on the interdependence of related behaviors sets behavior systems approaches apart from more analytical approaches in biology and psychology that treat

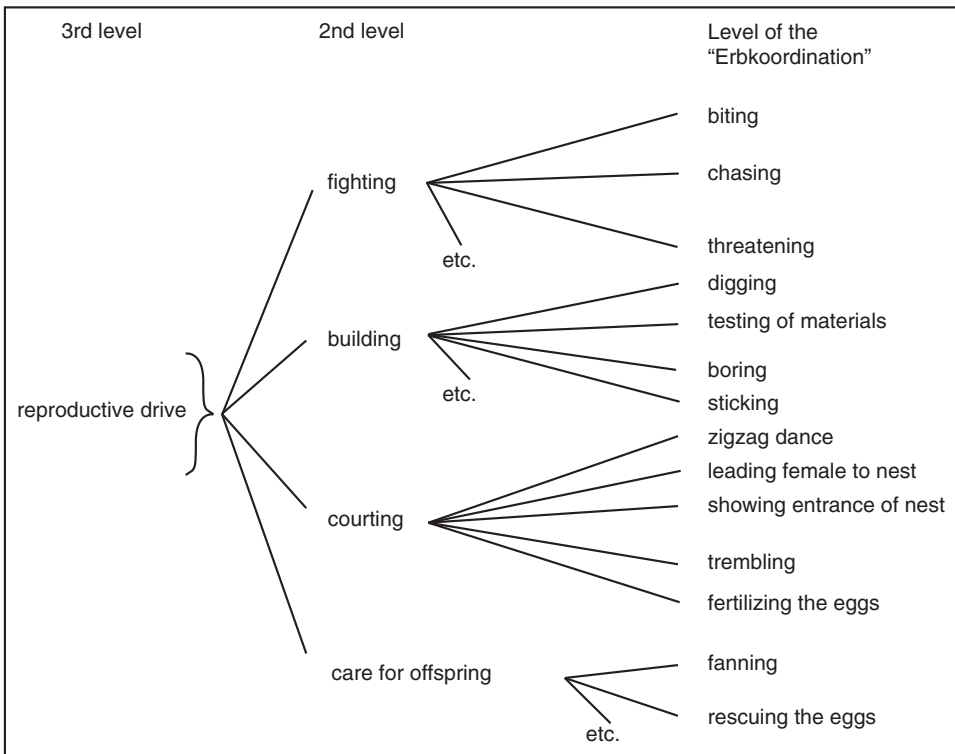
behavioral variables as discrete and independent. What began as a hypothesis about behavior being hierarchically organized matured into a set of methods concerned specifically with the functional organization of an animal's behavioral repertoire.

While the rest of ethology grew progressively more analytical over the twentieth century, Gerard Baerends (1941, 1976) retained focus on sequential relations among behaviors, how different behaviors interrelate temporally, and which situations lead to which responses. In Baerends' approach, one monitors behavior of animals in the wild for extended periods. Monitoring can be continuous or by sampling at regular intervals. Focus on the interrelation of behavioral forms invites use of advanced statistical or modeling techniques to identify patterns of concurrence. To clarify causation, field experiments are conducted where possible and necessary.

Although behavior systems approaches that followed differed from Baerends' in many respects, a central concern with situating behavior in a behavioral or motivational context is held in common.

### Model of the Animal

Behavior systems approaches involve multiple kinds of theory. At its most general, a behavior systems approach comprises a set of assumptions and a way of talking about them. It is not a

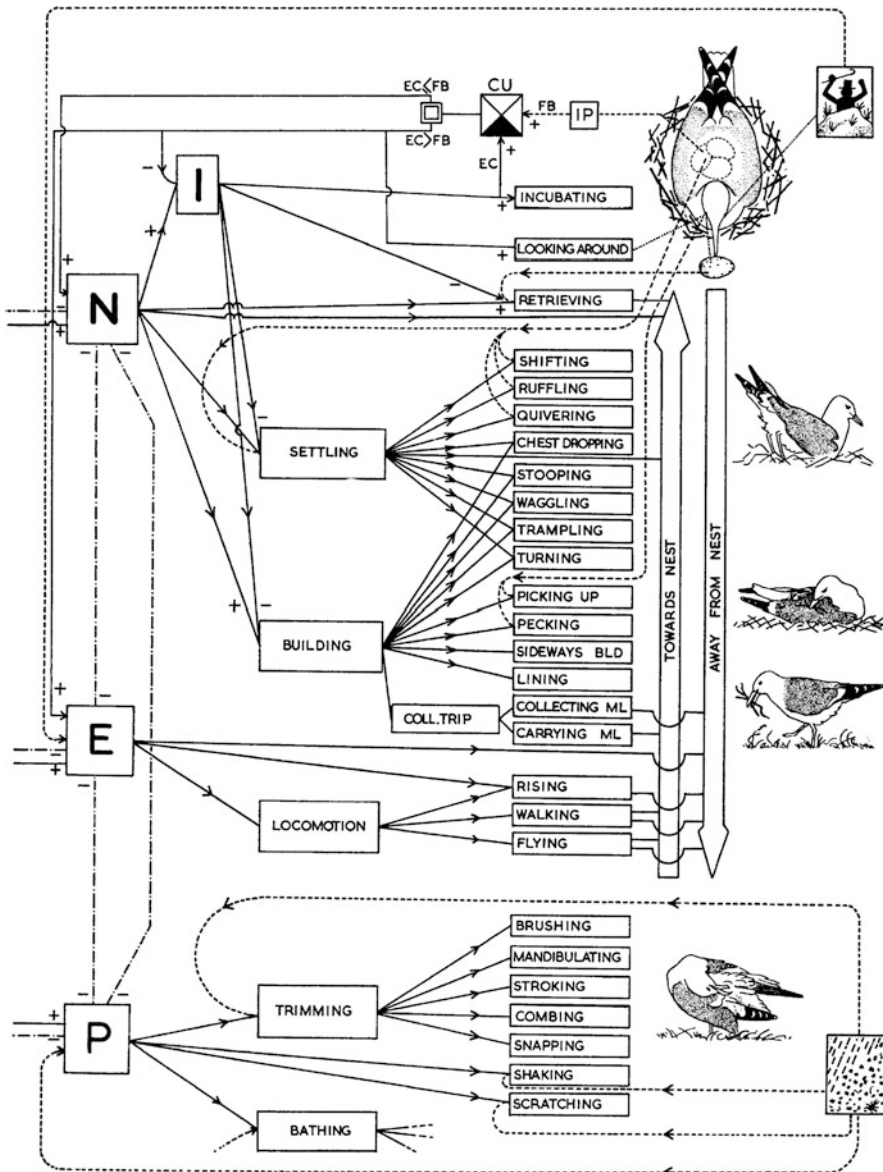


**Behavior Systems, Fig. 1** Tinbergen's 1942 hierarchy of moods model of the reproductive drive in stickleback fish (From Tinbergen 1942)

hypothesis to be tested, but a way of approaching behavior that embraces its complexity, focusing specifically on its organization. It is an interpretive and investigative strategy or framework.

One output of this strategy is a model of how the animal's behavior is organized. Figure 2 shows one such model. This model of the animal is also a kind of theory, but still not a theory in the familiar terms of species-general or system-general capacities or processes, like learning or reasoning, but of the species and system itself. This produces an apparent problem: such models are not in a form that is readily interpretable in terms of more common theories or familiar interpretive frameworks. While pondering the detailed models of herring gull nesting (Fig. 2) or digger wasp provisioning (Baerends 1941), which sometimes look like wiring diagrams, one is surely impressed, and perhaps awed by the work involved, but may then wonder what is to be done with such specific models of relatively obscure animals and systems.

The detailed models produced by such analyses are more than mere curiosities of natural history. With a theory of the animal and system in hand, one then has a basis upon which to situate further analyses and test hypotheses in more familiar terms, such as a theory about some cognitive phenomenon. Analyses of abstractly phrased capacities or processes can be embedded within an independently developed model of the specific animal's behavioral organization. This way behavior systems solves a problem for psychology that arises in any preparadigmatic science: some description should precede assessment of theories, but the terms of description (what is measured and what it means) are determined by the theory. Thus, without an independent foundation, abstractly phrased theories of capacities specify the terms of their own assessment. For instance, checking a food trough is often taken as an indicator of expectation of food, without concern for when that animal might otherwise perform the



**Behavior Systems, Fig. 2** Baerends' model of nesting behavior of herring gulls (From Baerends 1976)

same behavior. A behavior systems perspective solves this dilemma by providing a theoretical basis for description in terms specific to the animal, system, and circumstance.

This model of the animal approach, by which one first describes the structure of the behavior in a given system and then uses this to situate analyses of phenomena of interest, is a thormorphic approach (Timberlake 2007). It provides a manner

of foundation, but unlike chemistry, for instance, which has just one periodic table, the kind of foundation provided by a behavior systems framework is specific to the animal, system, and circumstance. This can be aptly contrasted with common alternative interpretive frameworks. One common way of interpreting behavior is by anthropomorphism, wherein one uses suppositions about human cognition or behavior as a

model to provide a basis for describing or understanding the behavior of other animals. The dangers of anthropomorphism have been aptly identified (as well as solutions to some of them), although explicit and implicit anthropomorphic approaches remain prevalent in animal cognition research. Another common approach bases analyses on normative theories. A fault with normative approaches is that they permit interpretation only of behaviors that are clearly and directly instrumental. The benefits of normative approaches can be recovered, however, by embedding such analyses in a behavior systems framework. In general, abstractly phrased approaches concerned with capacities tend to permit interpretation of only a very limited range of behavioral variables. A primary gain of alignment with a behavior systems approach is an ability to interpret a broader array of behaviors.

Behavior systems may be said to involve yet another level of theory insofar as one views a motivational system as a model the animal holds about the world. This aligns behavior systems, at least superficially, with “theory theories,” views that attribute a naïve theory to the animal, such as a “theory of mind” or “naïve physics” or *Umwelt*. A similar point can be made regarding some graphical model-based views, including those that assume that the animal forms a representational model of relevance relations. Caution is warranted when drawing analogies between naïve theories or graphical models, and motivational systems, for the terms are typically different. Still, such analyses may often be complementary.

## Evolution

Behavior systems is an evolutionary approach. Evolution is used to permit a connection with ecological pressures, similar to other evolutionary approaches in psychology. However, focus on systems and behavioral interrelations, as opposed to discrete behavioral traits, sets it apart from typical evolutionary approaches. The benefit of restricting evolutionary hypothesizing to interrelated components of systems is that it narrows

focus on local selection pressures. Modeling the structure of behavior systems relies heavily on evolutionary thinking, which it uses as a source of hypotheses, and to provisionally fill the many gaps in knowledge concerning perceptual, motor, and motivational factors. Admittedly, behavior systems are highly complex, with sensory, motor, and motivational components evolving in tandem, and this produces substantial uncertainty regarding the specific selection pressures and their impact on evolution. This problem, however, is not unique to behavior systems approaches.

## Behavior Systems/Neural Systems/Motivational Systems

Although behavior systems theory was developed within ethology as its leaders were working to establish ethology as a science of observable behavior, the earliest behavior systems models referred to drives or moods or nervous centers. In the context of sciences of behavior growing progressively uneasy about internal variables, this reference to unobservables drew fire. An early response to this was to talk literally about behavior, in functional terms, as contemporary ethology does. One sees this approach in Baerends’ work and thinking, and it is the more typical approach to take among ethologists.

Tinbergen’s (1951) own conception of behavior systems, in contrast, was primarily concerned with nervous structures. This view is echoed in the writing of later ethologists, such as Jerry Hogan (1994), as well as neuroscientists (e.g., Fanselow 1994). This conception of behavior systems has been criticized as physiologizing, but it has also produced some successes. Michael Fanselow (1994), for instance, applied such an approach to produce a model of defensive behavior in rats with reference to specific neural structures.

A third way of conceiving of behavior systems is closest to the initial formulations, in motivational terms. This is the more common approach among psychologists, notably William Timberlake (1983a, 1994, 2001) and Michael Domjan (1994), and the approach that has undergone the most development. This conception has



provided the basis for a theory of learning (below) and opens behavior systems analyses to investigation of cognition more generally.

One difficulty faced by views of behavior systems phrased in strictly behavioral terms, as opposed to motivational, is that the specific patterns of behavior an animal exhibits appear to depend heavily on the response supporting characteristics of the apparatus and the details of the procedure. Different circumstances may afford different manifestations of a given motivational status, and this adaptability to changing environmental demands is an important part of Timberlake's approach, which allows a behavior systems model to remain relevant outside of an animal's specific niche. The niche itself might vary widely. A strict behavioral phrasing appears to imply that behavior will be brittle, not adaptable to changing circumstances, whether considering the variability encountered within the niche or between the niche and evolutionarily unforeseen environments like a Skinner Box.

Baerends generally adopted an ethologists' attitude and attempted to develop his thormorphic models as situated within the species' niche and test them there. In such environments, the distinction between motivational and behavioral systems can be blurred. Timberlake, in contrast, primarily remained in the laboratory. He stressed that behavior exhibited in laboratory settings is no less natural or relevant to understanding the animal. Timberlake recognized the importance of the specifics of the apparatus and procedure for producing specific patterns of behavior, but there is no pretense, by this view, that a more naturalistic setting would necessarily be more appropriate. Where one is interested in helping to make sense of laboratory findings, a replication attempt may often be the place to start. Specific aspects of the apparatus may limit or otherwise constrain behavior in ways that produce patterns of behavior that appear to support some theory artificially (Timberlake 1983a). Identifying such cases has historically been among the clearest critical successes of behavior systems work.

Note that by Timberlake's usage, a behavior system refers not only to its motivational

component but to perceptual and motor components as well. The motivational component receives focus by this approach, depending on the specific problems addressed, but it is remembered to be embedded within the motor and perceptual realities of the animal. Behavior will depend on all of these factors, as well as the current circumstance.

## Timberlake's Theory of Learning

William Timberlake (1983a) applied a behavior systems approach to learning, and the resultant theory (confusingly) took the name, behavior systems theory. The primary innovation was a shift in the conception of the unconditional from discrete stimuli to systems. By behavior systems theory, learning is a means of finding a match between the structure of one's environment and the structure of internal motivational systems. Tinbergen and Lorenz had talked about learning in similar terms, but left these intuitions undeveloped.

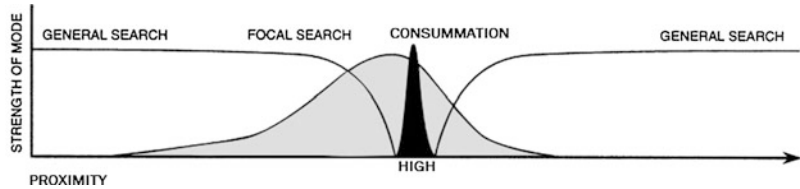
By a range of views, terminal feeding behaviors are reinforced through association with acquisition of food. By a behavior systems perspective this is only a part of a more complex system of behavior, the rest of which may be unsupported or even prohibited by the apparatus, or just not measured, for the purpose of isolating specific, quantifiable responses. Rather, when animals learn about associations in their respective worlds, they are learning how stimuli fit into a behavior system. An unconditional stimulus engages not just a single unconditional response but a whole motivational complex. An associated cue is fit into this complex.

## Three-Mode Model

Timberlake (1983a) presented the three-mode model which begins by dissociating three phases of system-specific behavior: consummatory, focal search, and general search. Earlier thinkers (Craig 1918; Konorski 1967; Bindra 1961) had dissociated consummatory (or terminal) from appetitive (or preparatory) behaviors. Consummatory (derived from the Latin, *cōnsummāre*: to complete, accomplish) responses are behavioral end

### Behavior Systems,

**Fig. 3** A depiction of the Silva-Timberlake model (From Silva et al. 1998a)



points, what happens when the goal is in hand, for example, killing the prey or copulating. These are the responses most typically in focus in conditioning studies, such as a pigeon's pecking a light that signals food. Appetitive behavior consists of the set of behaviors that lead the animal to such an end, such as hunting or courting. The three-mode model divides appetitive behavior further into focal search and general search. A predator's behavior changes strikingly when it spots prey. At that moment, the predator enters focal search mode, and they move in to kill, now focused on a particular target. However, the hunt had started long before this moment, as the animal exhibited a very different set of behaviors: general search. For some predators, general search manifests as roaming, some lie in wait. Each step in this sequence biases the animal differently in order to produce the conditions for the next phase, bringing the hunter progressively to a specific end. The animal solves a complex problem by dealing in sequence with just one segment of the problem at a time. Similarly, feeding on berries, one shifts between exploiting the current patch, searching locally for the next berry on a bough (focal search), and exploring, leaving the current patch to find the next (general search). This example accentuates the counter-intuitive point that feeding-related general search behavior often moves the animal away from food.

In addition to the response producing characteristics of motivational systems, Timberlake's approach stresses the response supporting characteristics of apparatus and procedure. Conditional responding can manifest in very different ways that depend not only on the significance the cue acquires to a system of behavior or motivation, which is related to the motivational significance of the US, the system evoked, involving such factors as temporal or spatial distance from the US, and

reliability of the CS-US relation, but also on the manner of response the environment affords. A consummatory conditional response is most likely when the CS is close, recent, and reliable in relation to the US. A general search CR is expected with long CS-US delays (e.g., Akins et al. 1994). If the CS is another rat, the behavior elicited is the social response connected with feeding; if the CS is a protrusion from the wall, manipulation and biting; if a moving sphere, chasing and grabbing and carrying (Timberlake and Grant 1975; Timberlake et al. 1982; Timberlake 1983b). Embedded in this analysis is a critique of general-process approaches insofar as they lose sight of how their procedures and apparatus produce patterns of behavior (Timberlake 1983a). More positively, behavior systems theory permits interpretation of a broader range of response forms that occur in conditioning studies and bringing these behaviors into an analysis gives it depth.

Although the three-mode model was developed in the context of feeding in rats, models with the same essential basis have been applied with success to sexual behavior in Coturnix quail (Domjan 1994) and fear behavior in rats (Fanselow 1994).

### Silva-Timberlake Model

Francisco Silva and Timberlake extended the three-mode model in an important way that places focus on the specific effects of temporal and spatial factors on motivational interactions. Figure 3 illustrates change in strength (vertical axis) of the three modes in relation to each other over a dimension of CS-US proximity (horizontal axis). This proximity dimension brings conceptual unity of various factors in conditioning studies, including temporal, spatial, correlational, and evolutionary relatedness. This basic model and its predictions

have proven surprisingly robust in application to conditioning phenomena (Silva et al. 1998a, b; Timberlake 2001).

## Connections with Other Sciences

Behavior systems theorists have long stressed integration of sciences and viewed behavior systems as means of accomplishing this. For Tinbergen (1951), it served as a theoretical link between ecological and physiological analyses and the basis for his first attempt to bring physiology into ethology. Timberlake's extensions of behavior systems (Timberlake 1983a; Timberlake 2001) provided a theoretical basis for principled integration of ethology with psychology. Both thinkers were also dedicated discipline bridge builders, investing heavily throughout their careers in providing institutional infrastructure to enable integration of sciences.

Throughout its history, depictions of behavior systems took the form of networks of interrelated drives or behaviors. These networks represented hierarchical organization, which was stressed in the initial presentations (e.g., Fig. 1), but behavior systems theorists otherwise took little inspiration from network theory. Similarly, the reference to systems was not principled application of systems theory. These potential connections remain unplumbed.

Gordon Burghardt has suggested that a behavior systems approach might be applied to emotions (Burghardt and Bowers 2017). The suggestion appears promising, but it awaits empirical support.

Robotics has contributed to the study of animal behavior methodologically by providing an independent means of testing hypotheses, and the two fields connect in the areas of synthetic biology and artificial life. Inspiration specifically from behavior systems thinking, particularly hierarchical organization and task decomposition, is apparent in the layered architectures used in some robotics communities, notably subsumption architecture (Brooks 1986). Layered architectures produced an initial boom in robotics research, permitting behavior-based robots to succeed at tasks that

had stumped earlier generations of robots. However, the initial success was followed by a bust, which may have been helped by better communication between these fields.

In general, a behavior systems approach can be viewed as a strategy for addressing questions throughout psychology, a portable foundation to carry around that is based on a model of the animal and system, rather than some general capacity, one that gives some guidance on how to apply abstract theories to real animals.

## Cross-References

- ▶ [Constraints on Learning](#)
- ▶ [Ecological Niche](#)
- ▶ [Evolution](#)
- ▶ [Francisco Silva](#)
- ▶ [Gerard Baerends](#)
- ▶ [Jerry Hogan](#)
- ▶ [Konrad Lorenz](#)
- ▶ [Michael Domjan](#)
- ▶ [Nikolaas Tinbergen](#)
- ▶ [Theromorphism](#)
- ▶ [William Timberlake](#)

## References

- Akins, C. A., Domjan, M., & Gutiérrez, G. (1994). Topography of sexually conditioned behavior in male Japanese quail (*Coturnix japonica*) depends on the CS-US interval. *Journal of Experimental Psychology: Animal Behavior Processes*, *20*, 199–209.
- Baerends, G. P. (1941). On the life history of *Ammophila campestris*. *Jur. Nederl. Akademie van Wetenschappen*, *44*, 483–488.
- Baerends, G. P. (1976). The functional organization of behaviour. *Animal Behaviour*, *24*, 726–738.
- Bindra, D. (1961). Components of general activity and the analysis of behavior. *Psychological Review*, *68*, 205–215.
- Brooks, R. A. (1986). A robust layered control system for a mobile robot. *IEEE Journal of Robotics and Automation*, *RA-2*, 14–23.
- Burghardt, G. M., & Bowers, R. I. (2017). From instinct to behavior systems: An integrated approach to ethological psychology. In J. Call, G. M. Burghardt, I. Pepperberg, C. Snowdon, & T. Zentall (Eds.), *APA handbook of comparative psychology* (Vol. 1,

- pp. 333–364). Washington, DC: American Psychological Association.
- Craig, W. (1918). Appetites and aversions as constituents of instincts. *Biological Bulletin*, *34*, 91–107.
- Domjan, M. P. (1994). Formulation of a behavior system for sexual conditioning. *Psychonomic Bulletin & Review*, *1*(4), 421–428.
- Fanselow, M. S. (1994). Neural organization of the defensive behavior system responsible for fear. *Psychonomic Bulletin & Review*, *1*(4), 429–438.
- Hogan, J. A. (1994). Structure and development of behavior systems. *Psychonomic Bulletin & Review*, *1*(4), 439–450.
- Konorski, J. (1967). *Integrative activity of the brain*. Chicago: University of Chicago Press.
- Silva, F. J., Timberlake, W., & Cevik, M. O. (1998a). A behavior systems approach to the expression of backward associations. *Learning and Motivation*, *29*, 1–22.
- Silva, F. J., Timberlake, W., & Gont, R. S. (1998b). Spatiotemporal characteristics of serial CSs and their relation to search modes and response form. *Animal Learning & Behavior*, *26*, 299–312.
- Timberlake, W. (1983a). The functional organization of appetitive behavior: Behavior systems and learning. In M. Zeiler & P. Harzem (Eds.), *Advances in analysis of behaviour* (Vol. 3, pp. 177–221). London: Wiley.
- Timberlake, W. (1983b). Rats responses to a moving object related to food or water: A behavior systems analysis. *Animal Learning & Behavior*, *11*, 309–320.
- Timberlake, W. (1994). Behavior systems, associationism, and Pavlovian conditioning. *Psychonomic Bulletin & Review*, *1*, 405–420.
- Timberlake, W. (2001). Motivational modes in behavior systems. In R. R. Mowrer & S. B. Klein (Eds.), *Handbook of contemporary learning theories* (pp. 155–209). Mahwah: Erlbaum.
- Timberlake, W. (2007). Anthropomorphism revisited. *Comparative Cognition and Behavior Reviews*, *2*, 139–144.
- Timberlake, W., & Grant, D. L. (1975). Auto-shaping in rats to the presentation of another rat predicting food. *Science*, *190*, 690–692.
- Timberlake, W., Wahl, G., & King, D. (1982). Stimulus and response contingencies in the misbehavior of rats. *Journal of Experimental Psychology: Animal Behavior Processes*, *8*, 62–85.
- Tinbergen, N. (1942). *An objectivistic study of the innate behaviour of animals*. Leiden: Brill.
- Tinbergen, N. (1951). *The study of instinct*. London: Oxford University Press.

# B

## Blocking

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## Definition

In the associative learning literature, blocking is typically defined as a deficit in responding to a conditioned stimulus (CS) that has always been paired with an unconditioned stimulus (US) in the presence of another CS previously established as a reliable predictor of the same US.

## Background

Until the late 1960s, it was generally assumed that the mere temporal and spatial contiguity between a CS and a US was a necessary and sufficient condition for conditioning to take place. The discovery of blocking by Leon Kamin (1968) was the first of a series of findings that defied this view, stimulating the development of modern learning theories. His seminal experiments on blocking relied in the experimental design summarized in Table 1. As can be seen, in this experimental design, subjects in both groups experienced the

same number of pairings between a light (L) and an electric shock. However, conditioned responding (CR) to the light was significantly stronger in the control group than in the experimental group. In other words, close contiguity between a conditioned and an unconditioned stimulus (L and the shock, in this case) did not suffice to produce strong conditioning.

According to Kamin (1968), this effect reveals that pairings of a CS and a US only give rise to conditioning if the US is unexpected. In the experimental group, when L is paired with the shock, this event produces little or no surprise, because the shock is readily predicted by a previously conditioned white noise (N). This is not the case in the control group, where the shock is completely unanticipated the first time L is presented. The idea that surprise drives learning was soon implemented in formal theories of associative learning. For instance, in the influential model of classical conditioning developed by Rescorla and Wagner (1972), surprise is represented as a prediction error, i.e., as the arithmetic difference between the “expected US” and the “experienced US.” In this model, the amount of learning supported by a conditioning trial is directly proportional to this difference.

Some models developed over the following years attempted to explain blocking by postulating different mechanisms. For instance, according to Mackintosh (1975), blocking can be explained by assuming that attention is biased toward predictive stimuli. In the case of the experimental

**Blocking, Table 1** Design summary of Kamin's (1968) blocking experiments

Group	Phase 1	Phase 2	Test	Result
Experimental	16 N – shock	8 LN – shock	L?	Weak CR
Control	–	8 LN – shock	L?	Strong CR

Note: N and L refer to a white noise and to the turning on of a house light, respectively; the unconditioned stimulus is a 1-milliampere electric shock; CR refers to conditioned responding

group in Table 1, when L and N are presented together for the first time, N is the most reliable predictor of the US and subjects will learn to pay more attention to it, leaving few attentional resources to process (and learn about) L. In a radically different vein, Miller and Matzel (1988) proposed that blocking is not due to a deficit in learning itself but to late processes related to the production of the conditioned response. In any case, as shown by these examples, offering a successful account of blocking soon became a touchstone for any theory of associative learning.

Although the blocking effect was initially explored in the area of animal conditioning, during the 1980s, several studies showed that it could also be detected in human predictive learning experiments (Dickinson et al. 1984). This led naturally to the conclusion that the mechanisms underlying different forms of human learning must be similar to the ones responsible for classical and operant conditioning in nonhuman animals. The following decades of research in human predictive learning were largely driven by the impetus provided by associative learning theories and animal conditioning research.

More recently, it has been suggested that blocking might not be the product of an associative learning process but rather the result of a simple deductive inference (De Houwer et al. 2002). If two conditioned stimuli predict a US, then presenting both of them together should predict and even more intense US. In a blocking design, however, the intensity of the US is exactly the same when only one CS is presented (N) and when two CSs are presented (L and N). Therefore, it can be concluded that one of the CSs (L) is not a predictor of the US. Consistent with this view, blocking seems to be sensitive to participants'

assumptions about the additivity of CSs (i.e., whether two CSs should predict a stronger US or not) or the maximality of the US (i.e., whether the intensity of the US is not changing because it is already happening at its maximal level). Manipulating these assumptions does not only affect blocking in human participants but also in non-human animals (Beckers et al. 2006). These findings have raised concerns about the validity of the whole associative learning framework, leading some authors to suggest that blocking and other learning effects are better understood in terms of propositional inference processes (Mitchell et al. 2009; but see Shanks 2010).

## Cross-References

- ▶ [Classical Conditioning](#)
- ▶ [Conditioned Response](#)
- ▶ [Conditioned Stimulus](#)
- ▶ [Contiguity](#)
- ▶ [Contingency](#)

## References

- Beckers, T., Miller, R. R., De Houwer, J., & Urushihara, K. (2006). Reasoning rats: Forward blocking in Pavlovian animal conditioning is sensitive to constraints of causal inference. *Journal of Experimental Psychology: General*, *135*, 92–102.
- De Houwer, J., Beckers, T., & Glautier, S. (2002). Outcome and cue properties modulate blocking. *Quarterly Journal of Experimental Psychology*, *55*, 965–985.
- Dickinson, A., Shanks, D., & Evenden, J. (1984). Judgment of act-outcome contingency: The role of selective attribution. *Quarterly Journal of Experimental Psychology*, *36*, 29–50.
- Kamin, L. J. (1968). "Attention-like" processes in classical conditioning. In M. R. Jones (Ed.), *Miami Symposium on the prediction of behavior, 1967: Aversive*



- stimulation* (pp. 9–31). Coral Gables: University of Miami Press.
- Mackintosh, N. J. (1975). A theory of attention: Variations in the associability of stimuli with reinforcement. *Psychological Review*, *82*, 276–298.
- Miller, R. R., & Matzel, L. D. (1988). The comparator hypothesis: A response rule for the expression of associations. In G. H. Bower (Ed.), *The psychology of learning and motivation* (Vol. 22, pp. 51–92). San Diego: Academic.
- Mitchell, C. J., De Houwer, J., & Lovibond, P. F. (2009). The propositional nature of human associative learning. *Behavioral and Brain Sciences*, *32*, 183–198.
- Rescorla, R. A., & Wagner, A. R. (1972). A theory of Pavlovian conditioning: Variations in the effectiveness of reinforcement and nonreinforcement. In A. H. Black & W. F. Prokasy (Eds.), *Classical conditioning II: Current research and theory* (pp. 64–99). New York: Appleton-Century-Crofts.
- Shanks, D. R. (2010). Learning: From association to cognition. *Annual Review of Psychology*, *61*, 273–301.

# M

## Medial Temporal Lobe

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### Structure and Connectivity

The medial temporal lobe (MTL) corresponds to the amygdala and the fifth temporal convolution of the human temporal lobe. The MTL cortex can be subdivided in the hippocampal formation and the surrounding cortex, the parahippocampal gyrus. The latter includes the entorhinal cortex, perirhinal cortex, and parahippocampal cortex (Squire and Zola-Morgan 1991; Zola-Morgan and Squire 1993). Important bidirectional pathways are established between high-order associative areas of the cortex and the MTL (Lavenex and Amaral 2000; Qin et al. 2016). The perirhinal cortex receives more prominent projections from unimodal associative areas such as the inferior temporal cortex and has efferents toward the lateral entorhinal cortex. The parahippocampal cortex receives inputs from multimodal associative areas such as the posterior parietal lobe and projects toward the medial entorhinal cortex. These two routes, commonly referred in the literature as the “what” and the “when” streams, finally converge in the hippocampus (Eichenbaum and Lip-ton 2008).

The hippocampal formation is a complex region with different cytoarchitectonical subregions including the subiculum, the hippocampus (also referred as the hippocampus proper or the Cornu Ammonis), and the dentate gyrus (Insausti and Amaral 2003). This structure has great synaptic plasticity properties, and it is the main site of adult neurogenesis in the brain (see chapter on the “► Hippocampus”). The hippocampus can be considered an information hub at the top of the hierarchy of the MTL system. Information can flow in and out the hippocampus from two main routes: (a) via subiculum (mediated by the entorhinal cortex) (Lavenex and Amaral 2000) and (b) via fornix (Aggleton et al. 2010). After hippocampal processing, information can be then output back to the parahippocampal gyrus through the subiculum and from there to the cortex. The fornix connects the hippocampus with subcortical areas including septal nuclei (particularly nucleus basalis of Meynert), mammillary bodies, anterior thalamic nuclei, ventral striatum, ventral tegmental area, locus coeruleus, and raphe nuclei. Additional direct afferents are received from the amygdala, which also has a connection to the hippocampus through the entorhinal cortex. Both hippocampi are connected through the commissure of fornix (also called hippocampal commissure), and the anterior commissure connects both medial temporal lobes.

Taking all together, these circuits and the particular cytoarchitectonical characteristics of the MTL allow establishing feedback and

feedforward connections with the cortex, which are essential for memory.

## The Role of MTL on Memory Processes

The pioneering work by Brenda Milner and colleagues evaluating patients with lesions in the MTL, including the iconic case of patient Henry Molaison (1926–2008), opened avenues for the investigation of the various aspects of memory that are causally linked to this area (Scoville and Milner 1957). H. M. had followed bilateral MTL removal for the relief of intractable temporal lobe epilepsy at the age of 27. Due to this treatment, he developed a severe amnesia. H. M. was unable to learn new information or form new memories – a condition called *anterograde amnesia*. Additionally, access to memories of events and facts occurring prior to the surgery was impaired to some extent – a condition called *retrograde amnesia*. This retrospective memory retrieval deficit occurred in a temporally graded manner, such that he was unable to recall almost anything from the 3 years prior to the surgery, but he was able to retrieve older memories. Such chronological pattern of impairment for autobiographical memory following MTL insult is known as the Ribot's Law (for a review, see Frankland and Bontempi 2005). Strikingly, general intellectual and perceptual functions were preserved as well as working memory, procedural memory, and *priming* (an implicit memory facilitation effect, whereby the exposure to certain stimuli affects the later response to other stimuli or tasks).

The publication of H. M.'s case, as well as other MTL lesion studies that followed, established the causal role of the MTL in *declarative memory* (explicit and conscious memory for facts and events). However, these studies were limited since lesions extended broadly to the anterior temporal lobe. Hence, such evidence did not allow isolating the specific contribution of each MTL structure. This fact prompted the development of animal models, followed by the use of neuroimaging techniques, which shed light on the functional properties of this region and fostered

the distinction between different memory systems.

Soon it was established that the memory deficits observed were related to the hippocampus and the surrounding parahippocampal gyrus, which will be hence referred to as the MTL memory system, excluding the amygdala and the lateral anterior temporal lobe (Squire and Zola-Morgan 1991; Zola-Morgan et al. 1991).

Today, the role of the MTL in long-term *episodic memory* (explicit encoding, consolidation, and recollection of experienced events including contextual details such as where, when, why, or with whom) is well established. For many years, a dominant view of memory recognition proposed subdividing recognition in two qualitatively distinct processes: familiarity and recollection (for a review see Yonelinas 2002). On the one hand, *familiarity* is a distributed process that follows the rules of signal detection, targeting a sense of knowing or having had previously experienced something. On the other hand, *recollection* is defined as an all-or-nothing process that may require the identification of details of an object or scene. Familiarity, recollection, and novelty processes were suggested to depend in different structures within the MTL (Daselaar et al. 2006). Accumulated evidence has shown that while the hippocampus is engaged in processing the details that lead to recollection, the surrounding perirhinal and parahippocampal cortex can support familiarity (for items and context, respectively) with certain independence of the hippocampus.

More recently, the growing interest on describing the particular elements that differentiate MTL structures' roles has led to a new approach. It considers that the core function performed by the MTL is the establishment of arbitrary associations, relational processing, or binding. Instead of building up on the psychological distinction between familiarity and recollection, researchers have begun to focus on the qualitative differentiation of MTL structures and a functional specialization dependent on the kind processed information (for a review, see Eichenbaum et al. 2012). One of the most influencing MTL function models in this vein is the Binding Item and

Context (BIC) model (Davachi 2006; Diana et al. 2007; Eichenbaum et al. 2007).

Based on neuropsychological and neuroimaging findings, the BIC model stresses the importance of binding during both encoding (Davachi 2006) and retrieval (Diana et al. 2007). According to this model, the perirhinal cortex supports the encoding of items and item features (intra-item associations) and plays a role in certain complex perceptual tasks (for a review, see Graham et al. 2010). On the other hand, the parahippocampal cortex supports the processing of the context in which items are presented. This context can include spatial (the “where”), temporal (the “when”), or even emotional information. All this information is finally transmitted through the entorhinal cortex into the hippocampus, which is the key structure that binds items and context across time and space into a single memory trace (inter-item associations).

## Spatial Navigation

Nevertheless, many different aspects and specifics of MTL function are still under debate. The exclusively long-term memory function of the MTL has been challenged. For instance, it has been suggested that the region also plays an important role in short-term memory (Ranganath and Blumenfeld 2005) and perception (for supporting and contrasting views see, Baxter 2009; Suzuki 2009).

One of the most relevant debates rises from specifying the main hippocampal function as spatial navigation in contrast to declarative memory (Eichenbaum and Cohen 2014). A long tradition in the rodent literature has focus on the spatial navigation function of the MTL including in the human (for a review see, Moser et al. 2008) since the discovery of place cells (in the hippocampus and parahippocampal cortex) (O’Keefe and Dostrovsky 1971) and grid cells (in the entorhinal cortex) (Fyhn et al. 2004). *Place cells* are neurons that fire when the animal is positioned at a specific spatial location. *Grid cells* are neurons that provide a position-in-space signal such as a cognitive representation of the space. From this perspective,

the MTL has a main role for both spatial memory and spatial navigation (Sanders et al. 2015).

More recently, neurons that fire at particular moments within a relevant time period have been identified in the hippocampus, namely, *time cells* (for a review, see Eichenbaum 2014). This has led some authors to suggest that the ultimate goal of the MTL may not be specific to the spatial navigation per se but rather reflect the integration and encoding of multiple details of the spatiotemporal context and the content of a given event that allows its differentiation from other events, whether they are pathways, sequences, or autobiographical memories (Eichenbaum and Lipton 2008; Eichenbaum et al. 2012).

## Amygdala

From an anatomical viewpoint, the amygdala is part of the medial temporal lobe. However, this independent nucleus is often excluded in most studies addressing the MTL function, which focus on the medial temporal lobe cortex (Squire et al. 2004). This is due to in part because the amygdala does not directly contribute to episodic memory or spatial navigation. Instead, the amygdala has received greater attention for its role in emotional processing, fear conditioning, and modulation of memory consolidation (LaBar and Cabeza 2006). More information on the function of this structure can be consulted in the appropriate chapter.

## Cross-References

- ▶ [Amygdala](#)
- ▶ [Declarative Memory](#)
- ▶ [Encoding](#)
- ▶ [Entorhinal Cortex](#)
- ▶ [Episodic Memory](#)
- ▶ [Hippocampus](#)
- ▶ [Navigation](#)
- ▶ [Parahippocampal Cortex](#)
- ▶ [Perirhinal Cortex](#)
- ▶ [Retrieval](#)
- ▶ [Spatial Memory](#)

## References

- Aggleton, J. P., O'Mara, S. M., Vann, S. D., Wright, N. F., Tsanov, M., & Erichsen, J. T. (2010). Hippocampal-anterior thalamic pathways for memory: Uncovering a network of direct and indirect actions. *European Journal of Neuroscience*, *31*(12), 2292–2307.
- Baxter, M. G. (2009). Involvement of medial temporal lobe structures in memory and perception. *Neuron*, *61*(5), 667–677.
- Daselaar, S. M., Fleck, M. S., & Cabeza, R. (2006). Triple dissociation in the medial temporal lobes: Recollection, familiarity, and novelty. *Journal of Neurophysiology*, *96*(4), 1902–1911.
- Davachi, L. (2006). Item, context and relational episodic encoding in humans. *Current Opinion in Neurobiology*, *16*(6), 693–700.
- Diana, R. A., Yonelinas, A. P., & Ranganath, C. (2007). Imaging recollection and familiarity in the medial temporal lobe: A three-component model. *Trends in Cognitive Sciences*, *11*(9), 379–386.
- Eichenbaum, H. (2014). Time cells in the hippocampus: A new dimension for mapping memories. *Nature Reviews Neuroscience*, *15*(11), 732–744.
- Eichenbaum, H., & Cohen, N. J. (2014). Can we reconcile the declarative memory and spatial navigation views on hippocampal function? *Neuron*, *83*(4), 764–770.
- Eichenbaum, H., & Lipton, P. A. (2008). Towards a functional organization of the medial temporal lobe memory system: Role of the parahippocampal and medial entorhinal cortical areas. *Hippocampus*, *18*(12), 1314–1324.
- Eichenbaum, H., Yonelinas, A. P., & Ranganath, C. (2007). The medial temporal lobe and recognition memory. *Annual Review of Neuroscience*, *30*, 123–152.
- Eichenbaum, H., Sauvage, M., Fortin, N., Komorowski, R., & Lipton, P. (2012). Towards a functional organization of episodic memory in the medial temporal lobe. *Neuroscience & Biobehavioral Reviews*, *36*(7), 1597–1608.
- Frankland, P. W., & Bontempi, B. (2005). The organization of recent and remote memories. *Nature Reviews Neuroscience*, *6*(2), 119–130.
- Fyhn, M., Molden, S., Witter, M. P., Moser, E. I., & Moser, M.-B. (2004). Spatial representation in the entorhinal cortex. *Science*, *305*, 1258–1264.
- Graham, K. S., Barense, M. D., & Lee, A. C. (2010). Going beyond LTM in the MTL: A synthesis of neuropsychological and neuroimaging findings on the role of the medial temporal lobe in memory and perception. *Neuropsychologia*, *48*(4), 831–853.
- Insausti, R., & Amaral, D. G. (2003). Hippocampal Formation. In *The human nervous system: Second edition* (871–914). Elsevier Inc.
- LaBar, K. S., & Cabeza, R. (2006). Cognitive neuroscience of emotional memory. *Nature Reviews Neuroscience*, *7*(1), 54–64.
- Lavenex, P., & Amaral, D. G. (2000). Hippocampal-neocortical interaction: A hierarchy of associativity. *Hippocampus*, *10*(4), 420–430.
- Moser, E. I., Kropff, E., & Moser, M. B. (2008). Place cells, grid cells, and the brain's spatial representation system. *Annual Review of Neuroscience*, *31*, 69–89.
- O'Keefe, J., & Dostrovsky, J. (1971). The hippocampus as a spatial map. Preliminary evidence from unit activity in the freely-moving rat. *Brain Research*, *34*, 171–175.
- Qin, S., Duan, X., Supekar, K., Chen, H., Chen, T., & Menon, V. (2016). Large-scale intrinsic functional network organization along the long axis of the human medial temporal lobe. *Brain Structure and Function*, *221*(6), 3237–3258.
- Ranganath, C., & Blumenfeld, R. S. (2005). Doubts about double dissociations between short- and long-term memory. *Trends in Cognitive Sciences*, *9*(8), 374–380.
- Sanders, H., Rennó-Costa, C., Idiart, M., & Lisman, J. (2015). Grid cells and place cells: An integrated view of their navigational and memory function. *Trends in Neurosciences*, *38*(12), 763–775.
- Scoville, W. B., & Milner, B. (1957). Loss of recent memory after bilateral hippocampal lesions. *Journal of Neurology, Neurosurgery & Psychiatry*, *20*(1), 11–21.
- Squire, L. R., & Zola-Morgan, S. (1991). The medial temporal lobe memory system. *Science*, *253*(5026), 1380.
- Squire, L. R., Stark, C. E., & Clark, R. E. (2004). The medial temporal lobe. *Annual Review of Neuroscience*, *27*, 279–306.
- Suzuki, W. A. (2009). Perception and the medial temporal lobe: Evaluating the current evidence. *Neuron*, *61*(5), 657–666.
- Yonelinas, A. P. (2002). The nature of recollection and familiarity: A review of 30 years of research. *Journal of Memory and Language*, *46*(3), 441–517.
- Zola-Morgan, S., & Squire, L. R. (1993). Neuroanatomy of memory. *Annual Review of Neuroscience*, *16*(1), 547–563.
- Zola-Morgan, S., Squire, L. R., Clower, R. P., & Alvarez-Royo, P. (1991). Independence of memory functions and emotional behavior: Separate contributions of the hippocampal formation and the amygdala. *Hippocampus*, *1*(2), 207–220.

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# B

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## Behavioral Levels

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The contemporary model of development, relational developmental systems (Overton and Lerner 2014), is very much grounded in Darwinian evolution, but not the modern synthesis of this position. One can understand the important role that ideas of evolution play in behavioral development without adopting a reductionist, determinist, or otherwise innate perspective (Lerner and Overton 2013; Lickliter 2016). Behavior develops and changes, a result of a myriad of influences (endogenous and exogenous) almost from the moment of conception and, based on current understanding of epigenetics (e.g., Moore 2015, 2016), perhaps before as well. Evolution, of course, is itself about change, and therein lies the crucial relationship between biology and psychology.

The fundamental law of Darwinian evolution is that change results from *natural selection*. But, as with all theories in science, Darwinian evolution has itself been subject to change and modernization. Accordingly, I follow Ho and Saunders in understanding *increasing complexity* (i.e., anagenesis) to be a second law of evolution after natural selection (Saunders and Ho 1976, 1981). Others who have adopted this line of

thinking (e.g., Stebbins 1969; Smith and Szathmáry 1995) did so from the perspective of the idea that there is a hierarchy of levels of increasing complexity and organization with evolution. Indeed, this idea can be considered “a central phenomenon of life” (Vrba and Eldredge 1984, p. 146). That this principle is extremely important in scientific understanding was recognized early by Pringle (1951) who noted that “The characteristic of living systems which distinguishes them most clearly from the non-living is their property of progressing by the process which is called evolution from less to more complex states of organization” (p. 175).

This hierarchical principle applies as well to the sciences which can be divided into areas of study based on qualitative changes in complexity of organization: physics and chemistry address lower levels of complexity; biology, psychology, and sociology address higher levels of complexity. This idea appears to have originated with Auguste Comte in the late 1800s (see Boorstein 1998, p. 223) and was subsequently developed in the twentieth century by others such as Novikoff (1945) and Feibleman (1954) (Greenberg and Partridge 2010; Greenberg and Tobach 1984), conceptualized as the “concept of integrative levels.” Aronson (1984) described this idea as a crucial organizing principle in science which is “. . . a view of the universe as a family of hierarchies in which natural phenomena exist in levels of increasing organization and complexity. Associated with this concept is the important corollary



that these successions of levels are the products of evolution. Herein lies the parallel with anagenesis” (p. 66).

In their important book, Michel and Moore (1995) noted that T. C. Schneirla, among the pre-eminent comparative psychologists of the twentieth century, applied this thinking to behavior invoking the idea of phyletic levels. Michel and Moore note that by advancing “the idea that the study of evolution could be informed by developmental analysis” (p. 120) Schneirla emphasized that both biology and psychology are developmental sciences. The historical record is clear that as evolution has continued it has resulted in increasingly more complex forms of animal life. In the context of this discussion it is evident that, with few exceptions, more recently evolved forms are more complex in their biology and their behavior than are earlier evolved forms. Schneirla pointed out that we can “begin to understand the differences between species by noting gross differences in behavioral complexity” (Michel and Moore 1995, p. 121) in a hierarchical relationship reflecting a strong correlation between both biological and psychological complexity.

Applying this idea to behavior, Tobach and Schneirla (1968) proposed an anagenetic, hierarchical ranking of behavioral levels across species, based loosely on the fact of increasing neural complexity with evolutionary advance. The behavioral levels are separated into two groups, one at which biological factors dominate behavior and one at which psychological and social principles become important. The levels they identified are: *Taxis*, at which behavior is under immediate stimulus control, an example of which is a moth flying toward a light source; *Biotaxis*, a higher level at which behavior is influenced not only by the immediate presence of a stimulus but also by the presence of biochemical sequelae from other organisms such as pheromones; and *Biosocial*, the level at which the social interaction of groups of animals plays an important role in organizing and regulating behavior. In Schneirla’s analysis of army ant behavior, he saw their cyclic activity to be a result of reciprocal social stimulation provided by the enormous number of individuals in an ant colony. That cyclic activity is absent in

single ants and is seen only when ants are together in large numbers; *Psychotaxis*: Psychology becomes important at this phyletic level in the form of mediation by past experience. Rosenblatt and Schneirla (1962) demonstrated with cats that the relationship between infant and mother begins with biotactic orientation by the kitten to its mother by means of tactile and olfactory stimuli. Subsequently, higher-order processes (e.g., learning and reinforcement) enter in at later stages of that relationship; *Psychosocial*: at this highest level behavioral organization is regulated by complex social bonds and social interactions characteristic of advanced vertebrates. Among primates, for example, lasting social bonds result from initial complex biosocial and biotactic interactions between an infant and a mother such as those involved in rocking, providing of contact comfort, and nursing.

Tobach and Schneirla (1968) ended their analysis with the description of the psychosocial level. There is, however, merit in developing the system somewhat further to differentiate among phyletic levels of primates and their corresponding communication behaviors. Whereas the behavior of all primates falls into the psychosocial level, at least with respect to communication there are less and more complex forms. All primates communicate, but a few individuals of some species have developed complex communication skills, bordering on true language (Savage-Rumbaugh et al. 1993). Accordingly, it seems appropriate to further subdivide the psychosocial level into three separate behavioral sub-groupings (Psychosocial I, II, and III; Greenberg and Haraway 2002), distinguished by the nature of communication complexity: a communication only, nonlanguage level (e.g., vervet monkeys); a proto-language level (e.g., chimpanzees and bonobos); and a true language level (only *H. sapiens*). Each of these behavioral levels is demarcated by the evolutionary appearance of species whose behavioral repertoires are increasingly more plastic and complex (Lerner 1984) as are their nervous systems. This ordering of these levels is similar to that of traditional phylogenetic taxonomies.

The utility of the application of this behavioral taxonomy can be seen in the way Greenberg and

**Behavioral Levels, Table 1** Levels of behavioral complexity displayed by major animal groups in feeding behavior

Major groups	Higher levels of complexity illustrated
<i>Protozoa</i>	Taxic
<i>Cnidaria</i>	Taxic
<i>Cnidaria</i>	Biotaxic, biosocial
<i>Echinodermata</i>	Biotaxic, biosocial
<i>Platyhelminthes</i>	Biotaxic, psychotaxic
<i>Molusca</i>	Biosocial, psychotaxic
<i>Arthropoda</i>	Biosocial, psychotaxic
<i>Osteichthyes</i>	Biosocial, psychotaxic
<i>Amphibia</i>	Biosocial, psychotaxic
<i>Reptilia</i>	Biosocial, psychotaxic
<i>Aves</i>	Psychotaxic, psychosocial
<i>Mammalia</i>	Psychotaxic, psychosocial

Haraway (2002) demonstrated its use for feeding behavior and its complexity across phyla and species. As animals became more complex with evolutionary advance, their nervous systems and feeding behavior became increasingly diverse and flexible. Table 1 lists major animal groups and shows at which behavioral (phyletic) levels their feeding behavior may be organized.

This notion is directed at the classification of behavior. Note that for most groups feeding behavior is organized at more than one level and that individual species can function behaviorally at more than one level (for example, at different stages in its development). Each animal then should be classified at its highest level of behavioral complexity in respect to a behavior, with the idea that a higher classification subsumes the levels below it. In Protozoa, such as the amoeba, feeding is regulated solely by the presence of appropriate chemicals at appropriate intensities; they are thus organized taxically for this behavior. Among the Cnidaria, such as Hydra, feeding is mostly a taxic process, although the ability of these animals to distinguish among living or recently living foodstuffs for prey suggests some biotaxic organization. Feeding by mollusks shows even higher organizational processes at work, allowing learning to become an influence of their feeding behavior. Among the vertebrates, feeding

complexity, the influence of conspecifics, and many components of learning (e.g., the remarkable caching ability of some birds) show their feeding behaviors to be organized at the highest levels. This organizational system was applied by Greenberg and Haraway (2002) to a full range of behaviors further attesting to its utility and is shown in Table 1.

The heuristic value of Schneirla's use of the levels concept in this way can be seen in replies to criticisms that have been leveled against it (Tobach and Greenberg 1984). Against hereditarianism, the concept poses the question about how genes might function at different levels; there is no special value placed on any level, succeeding levels integrate preceding ones, and the formulation of a question determines the appropriate level of inquiry; the concept does not imply anything about the "proper" research to be done as investigations are needed at all levels; the levels concept provides for the generation of critical hypotheses, especially regarding developmental issues; and finally, "the levels concept . . . belongs to the province of the science historian" (Tobach and Greenberg 1984, p. 6) which is reflected in the statements of Pringle and Aronson cited earlier in this entry.

## Cross-References

- ▶ [Approach/Withdrawal](#)
- ▶ [Comparative Psychology](#)
- ▶ [Development of Behavior](#)
- ▶ [Epigenesis](#)
- ▶ [Ethel Tobach](#)
- ▶ [Evolution](#)
- ▶ [Heritability of Behavior](#)
- ▶ [Language Research: Great Apes](#)
- ▶ [Primate Communication](#)
- ▶ [Protolanguage](#)
- ▶ [Psychosocial, Psychotaxis](#)

## References

- Aronson, L. R. (1984). Levels of integration and organization: A reevaluation of the evolutionary scale. In G.

- Greenberg & E. Tobach (Eds.), *Behavioral evolution and integrative levels* (pp. 57–81). Hillsdale: Lawrence Erlbaum Associates.
- Boorstein, D. J. (1998). *The seekers*. New York: Vintage.
- Feibleman, J. K. (1954). Theory of integrative levels. *British Journal for the Philosophy of Science*, 5, 59–66.
- Greenberg, G., & Haraway, M. M. (2002). *Principles of comparative psychology*. Boston: Allyn & Bacon.
- Greenberg, G., & Partridge, T. (2010). *Cognition, biology, and methods. volume 1 of the handbook of life-span development* (pp. 115–148). Editor-in-chief: R. M. Lerner. Hoboken: Wiley.
- Greenberg, G., & Tobach, E. (Eds.). (1984). *Behavioral evolution and integrative levels*. Hillsdale: Lawrence Erlbaum.
- Lerner, R. M. (1984). *On the nature of human plasticity*. Cambridge: Cambridge University Press.
- Lerner, R. M., & Overton, W. F. (2013). Epigenetics, evolution and embodiment: On the conceptual vacuity of evolutionary psychology. *OA Genetics*, 1(1), 6.
- Lickliter, R. M. (2016). Developmental evolution. *WIREs Cognitive Science*. doi:10.1002/wcs.1422.
- Michel, G. F., & Moore, C. L. (1995). *Developmental psychobiology*. Cambridge, MA: MIT Press.
- Moore, D. S. (2015). *The developing genome: An introduction to behavioral epigenetics*. New York: Oxford University Press.
- Moore, D. S. (2016). Behavioral epigenetics. *WIREs Systems Biology and Medicine*. doi:10.1002/wsbm.1333.
- Novikoff, A. (1945). The concept of integrative levels and biology. *Science*, 101, 209–215.
- Overton, W. F., & Lerner, R. M. (2014). Fundamental concepts and methods in developmental science: A relational perspective. *Research in Human Development*, 11, 63–73.
- Pringle, J. W. S. (1951). On the parallel between learning and evolution. *Behaviour*, 3, 174–215.
- Rosenblatt, J. S., & Schneirla, T. C. (1962). The behavior of cats. In E. S. E. Hafez (Ed.), *The behaviour of domestic animals* (pp. 453–488). London: Ballière, Tindall & Cox.
- Saunders, P. T., & Ho, M. W. (1976). On the increase in complexity in evolution. *Journal of Theoretical Biology*, 63, 375–384.
- Saunders, P. T., & Ho, M. W. (1981). On the increase in complexity in evolution II. The relativity of complexity and the principle of minimum increase. *Journal of Theoretical Biology*, 90, 515–530.
- Savage-Rumbaugh, E. S., Murphy, J., Sevcik, R. A., Brakke, K. E., Williams, S. L., & Rumbaugh, D. R. (1993). Language comprehension in ape and child. *Monographs of the society for Research in Child Development* (serial no. 233), 58(3–4), 1–252.
- Schneirla, T. C. (1949). Levels in the psychological capacities of animals. In R. W. Sellars, V. J. McGill, & M. Farber (Eds.), *Philosophy for the future* (pp. 243–286). New York: Macmillan.
- Smith, J. M., & Szathmáry, E. (1995). *The major transitions in evolution*. Oxford: England. W. H. Freeman.
- Stebbins, G. L. (1969). *The basis of progressive evolution*. Chapel Hill: University of North Carolina Press.
- Tobach, E., & Greenberg, G. (1984). The significance of T. C. Schneirla's contribution to the concept of levels of integration. In G. Greenberg & E. Tobach (Eds.), *Behavioral evolution and integrative levels* (pp. 1–7). Hillsdale: Lawrence Erlbaum.
- Tobach, E., & Schneirla, T. C. (1968). The biopsychology of social behavior of animals. In R. E. Cook & S. Levin (Eds.), *The biological basis of pediatric practice* (pp. 68–82). New York: McGraw-Hill.
- Vrba, E. S., & Eldredge, N. (1984). Individuals, hierarchies and processes: Towards a more complete evolutionary theory. *Paleobiology*, 10, 146–171.

# C

## Contingency

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### Definition

In the area of learning theory, the term *contingency* refers to the extent to which the presence of an event (the *predictor* event) is associated with changes in the probability of occurrence of another event (the *outcome* event).

### Main Text

Like correlation, the concept of contingency refers to the degree of covariation between two events. Although contingency can be measured in different ways, an extensively used index is  $\Delta P$  (Allan 1980), which measures the one-way dependency between two binary events. Specifically, for a predictor and an outcome that can be either present or absent this index is equal to the difference between the probability of the outcome event happening when the predictor event is present,  $P(\text{Outcome}|\text{Predictor})$ , and the probability of

the outcome event happening when the predictor event is absent,  $P(\text{Outcome}|\sim \text{Predictor})$ :

$$\Delta P = P(\text{Outcome}|\text{Predictor}) - P(\text{Outcome}|\sim \text{Predictor}) \quad (1)$$

We can estimate these two conditional probabilities from our repeated experience with the presence or absence of each of the events. Since the two events are binary, there are four possible combinations: (a) both the predictor and the outcome events occur together, (b) the predictor occurs and the outcome does not, (c) the predictor does not occur and the outcome occurs, and (d) neither the predictor nor the outcome occur. The frequency with which each of these four possibilities is experienced is typically summarized by constructing a contingency table (see Table 1). Once frequencies *a–d* are gathered, the conditional probabilities from Eq. 1 are easily calculated. The  $P(\text{Outcome}|\text{Predictor})$  is calculated by dividing the amount of occasions in which both the predictor and event occurred (*a*) by the total amount of times in which the predictor occurred (*a + b*). Analogously, the  $P(\text{Outcome}|\sim \text{Predictor})$  is calculated by dividing the amount of occasions in which only the outcome occurred (*c*) by the total amount of times in which the predictor did not occur (*c + d*). Therefore, Eq. 1 can be rewritten as:

**Contingency, Table 1** A contingency table depicting the four possible combinations of presence and absence of the predictor and the outcome

	Outcome	~Outcome
Predictor	<i>a</i>	<i>b</i>
~Predictor	<i>c</i>	<i>d</i>

$$\Delta P = \frac{a}{a+b} - \frac{c}{c+d} \quad (2)$$

The  $\Delta P$  index can take any value between -1 and +1. Positive values imply that the probability of the outcome event is higher when the predictor is present than when it is absent and, therefore, they are indicative of a positive statistical relationship. Negative values imply that the probability of the outcome is higher when the predictor is absent and they are indicative of a negative relationship. When the index takes a value of zero, the probability of the outcome is unaffected by the presence or absence of the predictor, that is, there is no statistical dependency between the two.

Robert A. Rescorla (1967, 1968, 1969) is known for stressing the central role of contingency in animal classical conditioning. He demonstrated that simple pairings of a neutral stimulus with an unconditioned stimulus did not suffice to guarantee that an association between the two would develop (note that in this context, the neutral stimulus acts as the *predictor* event and the unconditioned stimulus as the *outcome* event). According to the contingency approach to conditioning, for a neutral stimulus to develop an association with an unconditioned stimulus, the former must be able to predict changes in the probability that the latter will occur. That is, the contingency between the two must differ from zero. The greater the contingency, the stronger the expected associative strength. Moreover, the nature of the association will depend on the sign of the contingency: excitatory associations will form between stimuli for which the contingency is positive while inhibitory associations are anticipated if the contingency between the two is negative. In a series of classical fear conditioning experiments, Rescorla confirmed these

predictions, showing that rats were sensitive to the programmed contingency both respect to excitatory (Rescorla 1968) and to inhibitory (Rescorla 1969) conditioning (see also Murphy and Baker 2004 for a more recent example of contingency sensitivity in an appetitive conditioning preparation). This general framework can also explain the basic features of several associative learning effects like extinction, latent inhibition, or delayed reinforcement, as they all refer to situations where conditioned responding becomes weaker as a result of degrading the contingency between the predictor event and the outcome event. In any case, the topic is not free of controversy, and some authors have questioned the relevance of contingency in classical conditioning (Papini and Bitterman 1990; but see Baker et al. 2001).

Several studies have shown that human causal learning is also influenced by the contingency between the event that is presented as the potential cause (the predictor) and the effect (the outcome). In causal learning studies, participants are typically presented with a computerized task that asks them to find out to what extent a causal relationship exists (e.g., to what extent a pill is effective in curing a certain disease). After being exposed to several trials in which the presence and absence of the potential cause and of the effect are combined, participants are commonly asked to rate the intensity of the causal relationship existing between the two by making use of a numerical scale. In these experiments, causal ratings tend to be sensitive to the programmed contingency levels (e.g., Wasserman et al. 1993), although some consistent deviations from  $\Delta P$  are also observed. For instance, it has been observed that, for a given level of contingency, causal judgments tend to covary with both P(Outcome) and P(Predictor) (see Perales and Shanks 2007, for a review). Even in noncontingent situations, a conjunction of a high P(Outcome) and a high P(Predictor) tends to generate a strong impression of the predictor and the outcome being connected, giving rise to what researchers have called *illusions of causality* or *causal illusions* (see Matute et al. 2015, for a review).

## Cross-References

- ▶ [Classical Conditioning](#)
- ▶ [Conditioned Response](#)
- ▶ [Conditioned Stimulus](#)
- ▶ [Delay of Reinforcement](#)
- ▶ [Extinction in Learning](#)

## References

- Allan, L. G. (1980). A note on measurement of contingency between two binary variables in judgment tasks. *Bulletin of the Psychonomic Society*, *15*, 147–149.
- Baker, A. G., Murphy, R. A., Vallée-Tourangeau, F., & Mehta, R. (2001). Contingency learning and causal reasoning. In R. R. Mowrer & S. B. Klein (Eds.), *Handbook of contemporary learning theories* (pp. 255–306). Mahwah: Erlbaum.
- Matute, H., Blanco, F., Yarritu, I., Díaz-Lago, M., Vadillo, M. A., & Barberia, I. (2015). Illusions of causality: How they bias our everyday thinking and how they could be reduced. *Frontiers in Psychology*, *6*(888). doi:10.3389/fpsyg.2015.00888.
- Murphy, R. A., & Baker, A. G. (2004). A role for CS-US contingency in Pavlovian conditioning. *Journal of Experimental Psychology: Animal Behavior Processes*, *30*, 229–239.
- Papini, M. R., & Bitterman, M. E. (1990). The role of contingency in classical conditioning. *Psychological Review*, *97*, 396–403.
- Perales, J. C., & Shanks, D. R. (2007). Models of covariation-based causal judgment: A review and synthesis. *Psychonomic Bulletin & Review*, *14*, 577–596.
- Rescorla, R. A. (1967). Pavlovian conditioning and its proper control procedures. *Psychological Review*, *74*, 71–80.
- Rescorla, R. A. (1968). Probability of shock in the presence and absence of CS in fear conditioning. *Journal of Comparative and Physiological Psychology*, *66*, 1–5.
- Rescorla, R. A. (1969). Conditioned inhibition of fear resulting from negative CS-US contingencies. *Journal of Comparative and Physiological Psychology*, *67*, 504–509.
- Wasserman, E. A., Elek, S. M., Chatlosh, D. L., & Baker, A. G. (1993). Rating causal relations: Role of probability in judgments of response-outcome contingency. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *19*, 174–188.



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# C

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## Cognitive Bias

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### Definition

Cognitive bias refers to a systematic (that is, non-random and, thus, predictable) deviation from rationality in judgment or decision-making.

### Introduction

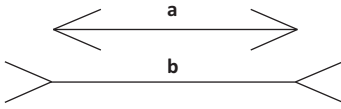
Most traditional views on human cognition propose that people tend to optimality when making choices and judgments. According to this view, which has been pervasive in many cognitive sciences (particularly Psychology and Economics), people behave like rational, close-to-optimal agents, capable of solving simple as well as complex cognitive problems, and to maximize the rewards they can obtain from their interactions with the environment. Generally, a rational agent would weight potential costs and benefits of their actions, eventually choosing the option that is overall more favorable. This involves taking into consideration all the information that is relevant for solving the problem, while leaving out any irrelevant information that could contaminate the decision (Stanovich 1999). Whole research areas in social sciences have been built upon this

assumption of rationality (see, e.g., the *Homo Economicus* theory in Economics).

However, this traditional view has been challenged in the last decades, in light of evidence coming from Experimental Psychology and related areas. Thus, a growing body of experimental knowledge suggests that people's judgments and decisions are often far from rational: they are affected by seemingly irrelevant factors or fail to take into account important information. Moreover, these departures from the rational norm are usually systematic: people fail consistently in the same type of problem, making the same mistake. That is, people seem to be irrational in a predictable way (Ariely 2008). Therefore, a theory that aims to model human judgment and decision-making must, in principle, be able to explain these instances of consistent irrationality or cognitive biases.

We can begin to examine the concept of cognitive bias by describing a similar, easier to depict, type of phenomenon: Visual illusions. Figure 1 represents a famous object configuration, the "Muller-Lyer illusion" (Howe and Purves 2005). The reader must observe the picture and decide which of the two horizontal segments, a or b, is longer.

In Western societies, most people would agree in that segment b looks slightly longer than segment a. In fact, despite this common impression, both segments a and b have exactly the same length. These segments only differ in the orientation of the adornments that round off the edges (i.



**Cognitive Bias, Fig. 1** The Muller-Lyer illusion (Adapted from Howe and Purves (2005) by the author)

e., “arrows” pointing inward or outward), which are responsible of creating the illusion that they have different lengths (Howe and Purves 2005). This example of a very simple visual illusion illustrates how people’s inferences can be tricked by irrelevant information (the adornments), leading to systematic errors in perception. A similar situation can occur across a variety of domains and tasks, revealing the presence of cognitive biases not only in perception but also in judgment, decision-making, memory, etc.

Typically, the consequence of cognitive bias is a form of irrational behavior that is predictable (because it is systematic). Cognitive biases have been proposed to underlie many beliefs and behaviors that are dangerous or problematic to individuals: superstitions, pseudoscience, prejudice, poor consumer choices, etc. In addition, they become specially dangerous at the group-level, since these mistakes are systematic rather than random (i.e., one individual’s mistake is not cancelled out by another one’s), leading to disastrous collective decisions such as those observed during the last economical crisis (Arieli 2009).

## Potential Causes

Traditionally, research on cognitive biases has tended to elaborate taxonomies, or lists of experimentally documented biases, rather than focusing on providing explicative frameworks (Hilbert 2012). Consequently, this is the way in which many textbooks and introductory manuals approach the topic: e.g., Baron (2008) lists a total of 53 biases in his introductory book to *Thinking and Deciding*.

Nonetheless, some authors attempted to offer coherent conceptual frameworks to understand what all these biases share in common and how

they originate. Here, we list some of the approaches that have tried to account for cognitive biases: limited cognitive resources, influence of motivation and emotion, social influence, and heuristics. They will be examined in turn.

## Limited Cognitive Resources

First, an obvious explanation for many reported cognitive biases is the limited processing capacity of the human mind. For example, since people’s memory does not possess infinite capacity, we cannot consider any arbitrarily big amount of information when we make an inference or decision, even if all this information is relevant to the problem. Rather, we are forced to focus on a subset of the available information, which we cannot process in detail either. Therefore, in most complex problems, the optimal, truly rational solution is out of reach and we can only aim at “bounded rationality” (Kahneman 2003), that is, making the best decision after taking into consideration a limited amount of information. This explanation works well to explain certain instances of cognitive bias, such as the problems associated to thinking with probabilities. In particular, research has documented that people tend to neglect base rate information when making Bayesian inferences (i.e., a cognitive bias). However, the same problem is solved much more easily when it is formulated in terms of frequencies, rather than in probabilities (Gigerenzer and Hoffrage 1995). The calculations become simpler in the latter case just because of the more natural presentation format, and the bias seems sensitive to this manipulation.

## Emotion and Motivation

Another potential cause for at least some cognitive biases is emotion or affect. Traditionally, research on decision-making understands rationality as “formal consistency,” conforming to the laws of probability and utility theory. Then, emotions are left out the rational decision-making process, as they can only contaminate the results.

However, subsequent research shows that emotions play a substantial role in decision-making (Bechara and Damasio 2005) and suggests that without emotional evaluations, decisions would never reach optimality. After all, emotions are biologically relevant because they affect behavior: e.g., we fear what can harm us, and consequently decide to avoid it. Several cognitive biases could be explained by the influence of emotions. For instance, the loss-aversion bias (Kahneman and Tversky 1984) consists of the preference for avoiding losses over acquiring gains of equivalent value, and it could be driven by the asymmetry in the affective value of the two types of outcomes. Other examples concern moral judgment. Many typical studies on moral judgment consist of presenting participants with fictitious situations such as the famous “trolley dilemmas” (Bleske-Rechek et al. 2010). In one simple variant of the problem, participants would be told that a trolley is out of control, barreling down the railways. Close ahead, there are five people tied up to the track. The participant could pull a lever to divert the trolley to a side track, in which there is one person tied up and unable to escape. Would the participant pull the lever? From a rational viewpoint, the utility calculus seems straightforward: it is preferable to save 5 people (and kill one) than the opposite outcome. Most people behave according to this utilitarian, rational rule. However, we know that the participants’ decisions in these dilemmas are sensitive to affective manipulations: for example, if the person who lies on the side track is a close relative of the participant (or their romantic partner), this would affect the decision (Bleske-Rechek et al. 2010). Therefore, emotions can drive some systematic deviations from the rational norm.

A related potential source of bias is motivation. Research has shown that people’s inferences can be biased by their prior beliefs and attitudes. That is, they can engage in motivated reasoning (Kunda 1990): when solving a task, they choose the beliefs and strategies that are more likely to arrive at conclusions that they want to arrive at. For example, participants who had to judge the effectiveness of gun-control measures to prevent

crime exhibited biased processing of contingency information to eventually align with their initial attitudes toward gun control (i.e., “motivated numeracy”) (Kahan et al. 2012). This could explain many other instances of bias in reasoning and behavior.

## Social Influence

Certain cognitive biases could be produced, or at least modulated, by social cues. For instance, Yechiam et al. (2008) examined the risk-aversion bias in a gambling task: typically, the bias consists of people preferring a sure outcome over a gamble of equivalent or higher value. Crucially, the researchers found that the bias was reduced when participants were observed by their peers. Other cognitive biases possess a more fundamental link to social cues. It is the case of the bandwagon bias, which describes the tendency of people to conform to the opinions expressed earlier by others, and which has strong influence in collective behaviors, such as voting in elections (Obermaier et al. 2015). So far, we do not know whether the contribution of social cues to this and related biases are due to people’s preference to conform to their peers or because people use others’ opinions as a source of information to form their judgments.

## Heuristics and Mental Shortcuts

Perhaps the most successful attempt to provide a coherent framework to understand cognitive biases is Kahneman and Tversky’s research program on heuristics (Kahneman et al. 1982). The rationale of this approach is as follows. First, making rational choices is not always feasible, or even desirable, for several reasons: (a) it takes time to effortfully collect and weight all the evidence to solve a problem; (b) it also needs the investment of lots of cognitive resources that could be used for other purposes; and (c) quite often a rough approximation to the best solution of a problem is “good enough,” whereas keeping on working to get the optimal solution is so

expensive that it does not pay off. Therefore, the mind uses heuristics, or mental shortcuts, to arrive at a conclusion in a fast-and-frugal way. A heuristic is a simple rule that does not aim to capture the problem in all its complexity or to arrive at the optimal solution, but that produces a “good enough” solution quickly, and minimizing the effort. At this point, we can recover the example of the Muller-Lyer illusion that we described above, to realize that it can be explained as a heuristic-based inference. In real life, people’s visual system must handle three-dimensional information to make inferences about distances and depth. This is highly demanding in terms of resources. However, the task can be simplified by looking for simple rules. Our cognitive system seems to interpret the visual input by making use of certain invariant features of the environment. In a three-dimensional world, two segments that converge at one point (as in Fig. 1) usually indicate a vertex (e.g., the edges formed by adjacent walls and ceilings typically display this configuration). The orientation of the edges can be used to predict whether the vertex is incoming (panel a) or outgoing (panel b) (first invariant). Furthermore, an edge far away from the observer will look smaller than one that is near (second invariant). In the real world that we navigate most of time, applying these two simple rules serves to correctly infer depth and distance, without implementing a costly information processing procedure. However, Fig. 1 is not a three-dimensional picture, and this is why applying the simple rules (heuristics) leads to an error or an illusion: incorrectly perceiving depth in a flat, bi-dimensional arrangement of lines and, thus, incorrectly judging the sizes of the segments. Nonetheless, Fig. 1 can be thought of as an exception, whereas most of visual configurations we see everyday actually confirm the simple rules, which explains why the heuristic is useful. In conclusion, as illustrated by the visual illusion example, judgment can be biased by the operation of heuristics that exploit regularities or invariants in the world. These heuristics are simple rules that can be expressed in an intuitive manner (such as “distant objects are seen smaller”) and need little time and effort to reach a conclusion (i.e., they are economic). While they

lead to conclusions that approximate a good enough solution most of the times, they can also lead to systematic mistakes.

A great deal of experimental research has documented several heuristics that could underlie many cognitive biases. Perhaps the most famous ones are the representativeness heuristic, the availability heuristic, and the anchoring-and-adjustment heuristic (Gilovich et al. 2002).

*Representativeness* This heuristic is based on similarity or belonging and can be intuitively formulated as “if A is similar to B (or belongs to group B), then A will work in the same way as B does.” That is, when an exemplar is perceived as representative of the group, all the features that are typical of the group are attributed to the exemplar. An example could be that of deducing that a given person is smart, just because he studies at the university or because he wears glasses. This heuristic can explain why people commit certain errors when solving Bayesian reasoning problems, such as the base-rate neglect (Bar-Hillel 1980).

*Availability* The availability heuristic is based on the ease with which a representation comes to mind. If a certain idea is easy to evoke or imagine, then it is incorrectly judged as likely to happen. A classical example is the reported overestimation of the likelihood of an airplane crash after watching a movie about airplane accidents. This heuristic can account for many common biases, such as recency bias: the piece of information that is the last in being presented is also the most easily remembered, and therefore it is usually weighted more heavily than other pieces of information, which can lead to serious errors in many domains (e.g., judicial). Another instance of the operation of the availability heuristic is the evaluation of near-win events: the fourth runner in crossing the finish line in a race often feels worse than the tenth one. This happens because this person can vividly imagine him/herself as being the third.

*Anchoring and Adjustment* This is sometimes considered as a special case of the availability heuristic. Knowing a tentative answer to a

question is known to bias further attempts to answer (these answers become closer to the anchor). For instance, imagine that you are asked the question: “in which year did Albert Einstein visit the USA for the first time?”. Let us assume that you do not know the answer, so you must guess. Most people would pick up a number like “1950.” Now, imagine that you are given a tentative range of years to answer. Research shows that people who are given a range of 1200 to 2000 actually answer with lower numbers than those who are given a range of 1900 to 2000. Respondents seem to use the range as a tentative response (anchor) and adjust their judgment away from it. The anchoring effect has been extensively studied in consumer behavior. For example, arbitrary numbers (i.e., the last digits of the participants’ social security numbers) can act as anchors to affect the amount of money that participants are willing to pay in exchange for a series of items (Ariely et al. 2003).

A further elaboration of the heuristics approach is the dual-system theory of human cognition (Kahneman 2013). According to this theory, the mind has two working modes: System I is fast, intuitive, heuristics-based, automatic, and frugal, whereas System II is slow, rational, optimality oriented, and resource-greedy. People perform many everyday tasks under System I: when the task is easy, when we need a quick solution, or when an approximate solution (not optimal) is good enough. However, certain task demands can activate System II. For instance, manipulations that reduce cognitive fluency, such as presenting the problem in a nonnative language, can lead to more thoughtful, rational, and bias-free solutions (Costa et al. 2014).

## An Evolutionary Perspective

A complementary line of research focused on understanding why cognitive biases appeared in first place in the evolution course, by analyzing their associated benefits. Thus, the error-management-theory (Haselton and Nettle 2006) proposes that cognitive biases (produced by heuristics or by

any other mechanism) were selected by evolution because they actually offer advantage for survival.

In ancestral environments, there is a pressure to make important, life-or-death decisions quickly (e.g., it is better to run away upon sighting a potential predator than to wait until it is clearly visible, but perhaps too close to escape). These conditions foster the development of decision mechanisms that (a) work fast and (b) produce the so-called “least costly mistake.” In this example, it is better to mistakenly conclude that a predator is in the surroundings than the alternative, i.e., mistakenly conclude that there is no predator. We know this because the two errors have very different consequences (it could be unnecessary waste of time in the former case and death in the latter) (Blanco 2016). Sometimes the least costly mistake is the less likely mistake, as it happens with the Muller-Lyer illusion above: most of times that we interpret colliding lines as three-dimensional vertexes, and as a cue to depth perception, we are right. In general, many cognitive biases seem to systematically favor the conclusion that aligns with the least-costly mistake, formulated in any of these ways.

Additionally, exhibiting certain cognitive biases can even produce other type of benefits, particularly in emotional terms. For example, one well-known cognitive bias is the illusion of control (Langer 1975), which consists of the mistaken belief that one can exert control over outcomes that are actually uncontrollable. The emotional consequences of this bias are noteworthy: a person who thinks that there is nothing that one can do to affect a relevant outcome might feel despair, or even depressed, for it is a sad realization that one has no control over his/her life. In contrast, those who develop the illusion of control (incorrectly) attribute to themselves any positive outcome that may happen, so they feel confident and safe. Furthermore, they will even feel motivated to keep trying and producing actions to affect the environment (i.e., the illusion of control produces behavioral persistence). In fact, evidence suggests that mildly depressed people are less likely to show the illusion of control (i.e., the depressive realism effect, Alloy and Abramson 1979), which

highlights the connection between cognitive biases and positive emotions.

In sum, at least some cognitive biases (like the illusion of control) seem to be associated to positive outcomes, or to the long-run minimization of costly mistakes, that could have represented an evolutionary advantage for our ancestors. Therefore, the traits that underlie the bias would have been selected through our evolutionary history.

Nonetheless, the error management theory has been received with some skepticism. Admittedly, typical cognitive biases not always align with the least-costly mistake. For instance, the same bias that facilitates the quick detection of a hidden predator (e.g., clustering illusion), thus protecting us from a serious threat, could also produce dangerous decisions in a different context, such as believing that a bogus health treatment, such as quackery, works (Blanco 2016).

## Conclusions

Cognitive biases have been defined as a general feature of cognition. As such, they are pervasive and can be observed in a vast variety of domains and tasks. Much has been studied about the impact of these biases on several key aspects of life. For example, cognitive biases could underlie highly societal issues, such as prejudice and racial hate (Hamilton and Gifford 1976), paranormal belief, or pseudomedicine usage (Blanco 2016), and more generally, the prevalence of poor decisions in many contexts, like consumer behavior (Ariely 2008).

Thus, it is not strange that researchers have tried to find out ways to overcome cognitive biases, a practice commonly known as “debiasing” (Larrick 2004; Lewandowsky et al. 2012). Different strategies have been used to develop debiasing techniques. Some are based on increasing the motivation to perform well (under the assumption that people can use normative strategies when solving tasks). Others focus on providing normative strategies to participants, so that they can replace their intuitive (and imperfect) approaches to a problem. Finally, other debiasing interventions take the form of

workshops to improve critical thinking and reasoning skills.

One common obstacle that debiasing efforts have encountered is called the “blind spot bias” (Pronin et al. 2002): While people can readily identify biases in others’ arguments, they find it difficult to detect similar biases in their own judgment. This is why transmitting the scientific knowledge about how cognitive biases work (and which factors affect them) can be a useful tool to complement debiasing strategies. In sum, advancing in our understanding of cognitive biases is in the interest of all society (Lilienfeld et al. 2009).

## Cross-References

- ▶ [Base-Rate Neglect](#)
- ▶ [Decision-Making](#)
- ▶ [Muller-Lyer Illusion](#)
- ▶ [Perception](#)
- ▶ [Problem-Solving](#)
- ▶ [Rationality](#)

## References

- Alloy, L. B., & Abramson, L. Y. (1979). Judgment of contingency in depressed and nondepressed students: Sadder but wiser? *Journal of Experimental Psychology: General*, 108(4), 441–485. doi:10.1037/0096-3445.108.4.441.
- Ariely, D. (2008). *Predictably irrational: The hidden forces that shape our decisions*. New York: Harper Collins. doi:10.5465/AMP.2009.37008011.
- Ariely, D. (2009, August). The end of rational economics. *Harvard Business Review*, 87(7), 78–84.
- Ariely, D., Loewenstein, G., & Prelec, D. (2003). “Coherent arbitrariness”: Stable demand curves without stable preferences. *The Quarterly Journal of Economics*, 118(1), 73–106. doi:10.1162/00335530360535153.
- Bar-Hillel, M. (1980). The base-rate fallacy in probability judgments. *Acta Psychologica*, 44(3), 211–233. doi:10.1016/0001-6918(80)90046-3.
- Baron, J. (2008). *Thinking and deciding*. New York: Cambridge University Press.
- Bechara, A., & Damasio, A. R. (2005). The somatic marker hypothesis: A neural theory of economic decision. *Games and Economic Behavior*, 52(2), 336–372. doi:10.1016/j.geb.2004.06.010.



- Blanco, F. (2016). Positive and negative implications of the causal illusion. *Consciousness and Cognition*. doi:10.1016/j.concog.2016.08.012.
- Bleske-Rechek, A., Nelson, L. A., Baker, J. P., Remiker, M. W., & Brandt, S. J. (2010). Evolution and the trolley problem: People save five over one unless the one is young, genetically related, or a romantic partner. *Journal of Social, Evolutionary, and Cultural Psychology*, 4(3), 115–127.
- Costa, A., Foucart, A., Arnon, I., Aparici, M., & Apestequia, J. (2014). “Piensa” twice: On the foreign language effect in decision making. *Cognition*, 130(2), 236–254. doi:10.1016/j.cognition.2013.11.010.
- Gigerenzer, G., & Hoffrage, U. (1995). How to improve Bayesian reasoning without instruction: Frequency formats. *Psychological Review*, 102, 684–704.
- Gilovich, T., Griffin, D., & Kahneman, D. (2002). *Heuristics and biases: The psychology of intuitive judgment*. New York: Cambridge University Press.
- Hamilton, D. L., & Gifford, R. K. (1976). Illusory correlation in interpersonal perception: A cognitive basis of stereotypic judgments. *Journal of Experimental Social Psychology*, 12, 392–407.
- Haselton, M. G., & Nettle, D. (2006). The paranoid optimist: An integrative evolutionary model of cognitive biases. *Personality and Social Psychology Review*, 10(1), 47–66. doi:10.1207/s15327957pspr1001\_3.
- Hilbert, M. (2012). Toward a synthesis of cognitive biases: How noisy information processing can bias human decision making. *Psychological Bulletin*, 138(2), 211–237. doi:10.1037/a0025940.
- Howe, C. Q., & Purves, D. (2005). The Müller-Lyer illusion explained by the statistics of image-source relationships. *Proceedings of the National Academy of Sciences of the United States of America*, 102(4), 1234–1239. doi:10.1073/pnas.0409314102.
- Kahan, D. M., Peters, E., Dawson, E. C., & Slovic, P. (2012). *Motivated Numeracy and Enlightened Self-Government* (Working Paper No. 307). New Haven: Yale Law School.
- Kahneman, D. (2003). A perspective on judgment and choice: Mapping bounded rationality. *American Psychologist*, 58, 697–720. doi:10.1037/0003-066X.58.9.697.
- Kahneman, D. (2013). *Thinking, fast and slow*. New York: Penguin Books.
- Kahneman, D., & Tversky, A. (1984). Choices, values, and frames. *American Psychologist*, 39(4), 341–350. doi:10.1037/0003-066x.39.4.341.
- Kahneman, D., Slovic, P., & Tversky, A. (1982). *Judgment under uncertainty: Heuristics and biases*. London: Cambridge University Press.
- Kunda, Z. (1990). The case for motivated reasoning. *Psychological Bulletin*, 108(3), 480–498.
- Langer, E. J. (1975). The illusion of control. *Journal of Personality and Social Psychology*, 32(2), 311–328. doi:10.1037/0022-3514.32.2.311.
- Larrick, R. P. (2004). Debiasing. In D. J. Koehler & N. Harvey (Eds.), *Blackwell handbook of judgment and decision making* (pp. 316–337). Oxford: Blackwell.
- Lewandowsky, S., Ecker, U. K. H., Seifert, C. M., Schwarz, N., & Cook, J. (2012). Misinformation and its correction: Continued influence and successful debiasing. *Psychological Science in the Public Interest*, 13(3), 106–131. doi:10.1177/1529100612451018.
- Lilienfeld, S. O., Ammirati, R., & Landfield, K. (2009). Giving debiasing away: Can psychological research on correcting cognitive errors promote human welfare? *Perspectives on Psychological Science*, 4(4), 390–398.
- Obermaier, M., Koch, T., & Baden, C. (2015). Everybody follows the crowd? Effects of opinion polls and past election results on electoral preferences. *Journal of Media Psychology*, 1–12. doi:10.1027/1864-1105/a000160.
- Pronin, E., Lin, D. Y., & Ross, L. (2002). The bias blind spot: Perceptions of bias in self versus others. *Personality and Social Psychology Bulletin*, 28, 369–381.
- Stanovich, K. E. (1999). *Who is rational? studies of individual differences in reasoning*. Mahwah: Erlbaum.
- Yechiam, E., Druryan, M., & Ert, E. (2008). Observing others’ behavior and risk taking in decisions from experience. *Judgment and Decision making*, 3(7), 493–500.

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# C

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## Cartesian Dualism

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### Definition

A philosophic doctrine originating from Descartes stating that there are two categories of things in existence, the physical and the mental.

### Introduction

Cartesian dualism was created by Descartes, a seventeenth-century Frenchman who made significant contributions to philosophy, mathematics, and science. He is primarily known as the father of modern philosophy and a key figure in the scientific revolution due to his mathematical legacy, weakening of the church's influence on philosophy, and inspiring future scientists like Newton. One of his greatest contributions to philosophy was his revival of several key philosophy debates from the Greeks, including that of monism versus dualism. The doctrine of monism asserts that everything in existence can fit within one category, or type, of "thing." Monism has two primary facets: materialism and idealism. Materialism is the theory that all things are physical in nature. Idealism is the less popular belief that all things are primarily from a mental plane.

Sometimes this is characterized as coming from an ideal plane. Dualism is the opposing view that there are two distinct kinds, or types, of things that are needed to characterize all of existence. While there are many proposed pairs of types, the distinction remains between physical and non-physical things.

### The Context of Cartesian Dualism

Descartes was both a philosopher and scientist during a critical point in the renaissance. While religion and theology had dominated philosophy, society, and acceptable knowledge, science was now rapidly expanding both its tools and its acclaim. Descartes began to explore the relationship between the mind and the body. He held both theology and religion, as well as mathematics and the scientific study of the laws and nature, in high regard but struggled to bring such disparate methods together. For him, this presented the need for dualism to explain the validity of both the aforementioned as they do not focus on the same type of thing.

### The Creation of Cartesian Dualism

In his book *Discourse on the Method*, Descartes famously introduces his doubt argument, with the well-known conclusion "Cogito ergo sum" or "I think therefore I am" (Descartes 1637/2007, p.

16). This lays the groundwork for dualism and the necessity of dualism. In the doubt argument, Descartes sets out a thought problem he utilized to search his own beliefs and purge any that he was not confident were true. Through this process of doubt, Descartes introduces many challenges to the truth of our own experience and thought, such as the idea that our current existence is just a dream and a malevolent demon giving us our sensations and perceptions and tricking us into believing that they are our own. This made Descartes doubt the vast majority of his beliefs. He could doubt all of physical reality, all of his sensations, but believed he could not doubt that he himself is mentally doubting all of these things. From this, he is assured that he exists because he is committing this act of doubting. If he can doubt all that is physical, but he cannot doubt this act his mind is committing, then there are different properties, and thus two different types of things are needed (Descartes 1637/2007). This argument was a convincing defense of the necessity of dualism, allowing Descartes to move the Greek notion of dualism away from matter and intellect and move it toward matter and consciousness. This is sometimes referred to as Descartes first argument for the separation of the mind and body.

In the Sixth Meditation of Descartes' *Meditations on First Philosophy*, he offers additional arguments to reinforce that the mind and body are separate. Descartes asserts that if two things are perceived to be separate, and to have different properties, they are not the same type of thing (Descartes 1641/2007, p. 30). This is followed by Descartes stating that he perceives with certainty that he exists as a thinking thing. He also perceives with near certainty that his physical body is not a thinking thing (Descartes 1641/2007, p. 30). From this he derives that the mind and body must be different because they have different properties, and he perceives them as different. Secondly, Descartes asserts that while the physical body is divisible into parts that then make up the whole, the mind is not indivisible, once again showing different properties that require them to be separate types of things (Descartes 1641/2007, p. 33). With these arguments, Descartes set the stage for the modern mind-body

problem, where the relationship and distinction between what is part of the mind and what is part of the body, or if they are even truly separate, are still contended.

Once the mind is considered separate from the body though, many questions are still left unanswered. In a later book *Treatise on Man*, Descartes more directly outlines his new form of dualism. He explains that the human body was created by God and works like an "earthen machine" (Descartes 1998, p. 1). Since the body is made of matter, it can be explained in purely mechanical terms and is subject to the laws of nature, such as those outlined by physics, like a machine is made up of various systems to perform specific operations such as breathing, eating, and walking (Descartes 1998). This mechanistic view of how the body functions seems very in line with our modern scientific perspective of our biological systems, as well as neurological systems and reflexes. Descartes himself was the first to propose a mechanism for which human behavior could be produced from and proposed the simple reflex was the building block for the behavior of the body and for animals that did not possess a mind explained their behavior completely (Skinner 1931). Similar to his contemporary, William Harvey, who first proposed the circulation of blood in *Exercitatio Anatomica de Motu Cordis et Sanguinis in Animalibus*, Descartes proposed a system within the body that circulated animal spirits where reflex actions resulted from a stimulus and the flow of animal spirits to nerves it caused (Descartes 1998, p. xxiv). This gave him a rough system that explained physical beings in terms of machines, for both humans and animals, and explained their actions including that of the brain. The only exception then was the mind. The mind being nonmaterial did not need to obey the laws of nature and escaped the rules of science and instead resided in the realm of theology. This made dualism an issue of theology versus physics and science for Descartes. These two fields were both very influential on Descartes' life, and his time period, but were at odds. This provided a solution to this as each focused on one facet of Cartesian dualism and thus has two completely separate content areas. Theology was what

characterized and studied the mind, the existing immaterial souls and spirits, as well as moral and ethical concerns. Physics was then relegated to modeling the physical phenomenon of the material things and there it stayed.

## Interactionism

With Cartesian dualism outlining two completely different types of substances, the problem of how they can coexist and could interact arises as a problem. Humans have both a constant experience of the physical world that has an easier time being objectively characterized and communicated, but we also have a constant experience of our mind as humans doubt and think. The difficulty in accounting for the ability for these two different substances to interact is a vulnerability that drove many thinkers to reject dualism and favor forms of monism instead. Descartes attempts to clarify this ambiguity in the Sixth Meditation of his *Meditations on First Philosophy*. The majority of dualist theories preceding Descartes were unidirectional, stating that the mind, or equivalent immaterial side, was superior to the physical able to overrule its laws and was the origin of our highest abilities. Descartes continued this, privileging the mind as the superior of the two, but thought of them as being able to reciprocally affect each other (Descartes 1641/2007). For example, basic needs not being met for the body, like severe hunger, could start to influence the mind as we lose focus on anything but food. Cartesian dualism clarifies the difference between the brain and the mind with the brain being material and the mind immaterial; functions of the brain could potentially affect the mind. Strong emotions are a function of the brain that could lead the body to overwhelm the rational mind as the emotions affects our behavior and thoughts.

Even with the relationship between the two clarified, the matter of how, and where, these separate substances can interact still had to be addressed. In the *Treatise of Man*, Descartes asserts that the location for this interaction was the pineal gland, a small endocrine gland with the

shape of a pine cone that is located near the center of the human brain (Descartes 1998). What drew Descartes' attention to the pineal gland were mainly false assumptions of the anatomy of the brain, some of which were already disproven in his time. Descartes believed that the pineal gland was held between the ventricles and surrounded by small arteries that brought it the animal spirits aforementioned (Descartes 1998, Figs. 54 and 55). He also thought that the pineal gland is not lateralized at the time it was thought to be one of the few parts of the brain that did not have symmetry across both sides of the brain, and it seemed central. Among his contemporaries, the pineal gland was not thought to have special qualities to give it such an exalted status.

## Implications for Nonhuman Animals

With the cognition of animals already being heavily discredited as anything complex, there was little interest in further research, and Descartes considered them to have no amount of mind. The religious values of the day viewed animals as soulless, lesser beings, and Descartes considered them to be purely constituted by material, physical things. This for Descartes meant animals were not complex enough to think, or doubt, and he even doubted their true ability to feel pain as he thought of them as purely driven by reflexes. His involvement in this topic was a strong push for human chauvinism in regard to comparative cognition and set the stage for centuries of scientific inquiry to work under the presumption that animals were fundamentally lesser. With this, animals were treated like they were inanimate objects, and all rules regarding ethical treatment were thus an unnecessary measure.

## Modern Context

Within the modern world, dualism has fallen into a minority view within academia, with physical monism now being the accepted view for the body of science. Dualism though is still in many ways an intuitive view that holds a lot of attraction to a

general audience. Many religious beliefs require a degree of dualism as things that fundamentally differ from the physical world are purported, such as a soul or any other aspect of a being that is unchanging and carries on beyond a body. There are also many nonreligious discussions that are prone to dualism. For example, complex issues involving the mind such as consciousness tend to have elements that intuitively feel different than something categorically physical, such as what makes humans conscious and how could anything physical create a sensation of experience that we have as conscious being. So while dualism is not normally accepted within the scientific tradition, it is still a prevalent position in modern day. Cartesian dualism is itself rarely believed in an unmodified form and instead is referenced for its historic influence on setting the context for the mind-body problem and modern solutions to it, whether with dualism or monism.

Since Cartesian dualism was first proposed, there have also been many breakthroughs in both the philosophy of mind and science in general that now affect how we view Cartesian dualism and the mind-body problem. Darwin's theory of evolution proposed in *On the Origin of Species* was a huge step in science and profoundly affected Cartesian dualism and the mind-body problem. Evolution links our development as a species to the rest of the living organism that inhabit the planet, undermining the idea that humans are innately superior in terms of mind and intelligence as we are closely related to other animals. This makes the existence of the mind more nuanced than Descartes' conservative stance that nothing but humans existed outside of the physical and reflexes. Advances in neuroscience also stand against much of Descartes' assertions around our neuroanatomy. Our understanding of our nervous system, including the brain, has greatly increased, disproving the idea of a system of nerves full of animal spirits and finding no evidence of the pineal gland being this special point where the mind and body are linked. We have also seen the mind-body problem be addressed in many different ways and recontextualized by philosophers such as Immanuel Kant, Thomas Huxley, and John Searle. Lastly, as the scientific study of

consciousness has risen as a field with the works of researchers like David Chalmers who created the "hard problem" and put the mind-body problem into a new context (Chalmers 1995).

Due to the rapid growth of technology in the modern age, we further have an obscuration of the line between what is mind and what is body. New interfaces are constantly being made that push the limits of our definitions as we develop integration between the organic and the artificial. This is shown with technology like synthesized and mechanical organs, as well as prosthetics that are controlled by our thoughts and neural activity. Examples like the aforementioned have called into question what should be considered part of a person or the environment or part of their mind. With this as well as advancement in the technology, we have to measure the activity of the brain; the mind-body problem naturally had to shift in the modern era in reaction to development in society and science.

## Conclusion

Cartesian dualism revived the Greek debate of monism vs. dualism and brought the focus of dualism away from intellect and toward consciousness setting the stage for the modern mind-body problem. The rise of Cartesian dualism additionally helped give a conceptual structure to the rapid growth of science in Descartes' era as it managed to embrace the laws of physical science and the mechanistic view of humans as constituted by systems with specific purposes. And it still maintained a place for the religious view of the immaterial soul, and superiority of humans over other animals, which characterized his time period. Currently though, Cartesian dualism, and dualism in general in academia, has fallen out of acclaim. The questions brought up by Cartesian dualism concerning what constitutes humans, and what is part of the body and what is part of the mind, continue to be extremely relevant in the modern age.

## Cross-References

- ▶ [Comparative Cognition](#)
- ▶ [Comparative Psychology](#)
- ▶ [Consciousness](#)
- ▶ [Meta-cognition](#)
- ▶ [Self-Awareness](#)
- ▶ [Theory of Mind](#)

## References

- Chalmers, D. J. (1995). Facing up to the problem of consciousness. *Journal of Consciousness Studies*, 2(3), 200–219. Retrieved from <http://consc.net/papers/facing.html>
- Descartes, R. (1637/2007, November). In J. Bennet (Ed. & Trans.), *Discourse on the method of rightly conducting one's reason and seeking truth in the sciences* (Part Four). Retrieved from <http://www.earlymoderntexts.com/assets/pdfs/descartes1637.pdf>
- Descartes, R. (1641/2007, April). In J. Bennet (Ed. & Trans.), *Meditations on First Philosophy in which are demonstrated the existence of God and the distinction between the human soul and body* (Sixth Meditation). Retrieved from [http://www.earlymoderntexts.com/assets/pdfs/descartes1641\\_3.pdf](http://www.earlymoderntexts.com/assets/pdfs/descartes1641_3.pdf)
- Descartes, R. (1998). Treatise on man. In S. Gaukroger (Trans.), *The world and other writings* (pp. 99–170). Cambridge: Cambridge University Press.
- Skinner, B. F. (1931). The concept of the reflex in the description of behavior. *Journal of General Psychology*, 5, 427–458. doi:10.1080/00221309.1931.9918416.



# A

## Afferent and Efferent Impulses

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### Synonyms

[Sensory and motor impulses](#)

### Definition

Neural impulses which travel from sensory organs/receptors to the central nervous system (CNS) are known as afferent impulses, whereas those which travel from the CNS to the organs/glands are known as the efferent impulses.

### Introduction

Those nerve cells which help in communication of action potentials (neural impulses) between the central nervous system and other body organs form the part of peripheral nervous system (PNS) (Baars and Gage, 2010). Depending upon the direction of this signal, neural impulses can be divided into two:

- (a) Afferent: neural impulse carries signals from sensory receptors or organs to the brain or spinal cord (CNS) for their further processing/analysis and
- (b) Efferent: neural impulse carries signals from brain or spinal cord (CNS) to the organs (like limbs, muscle, glands, etc.) for displaying proper reaction.

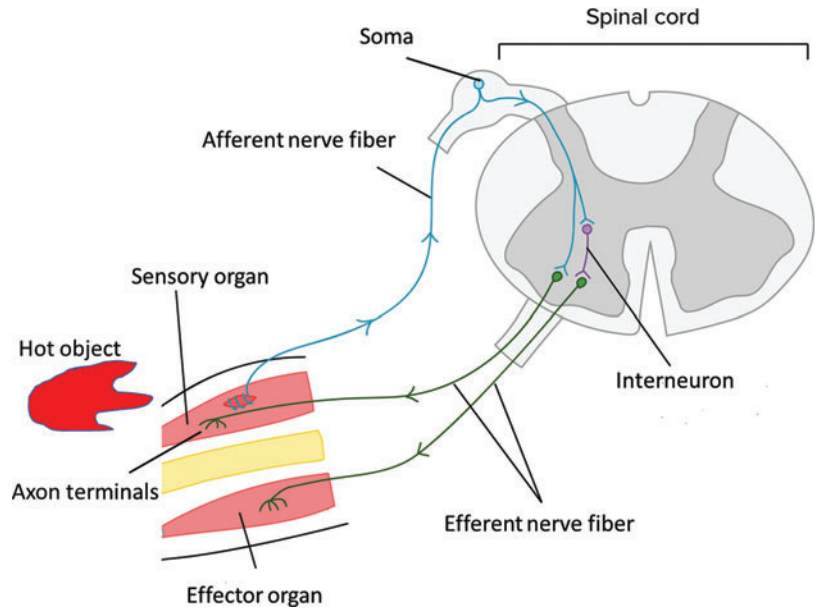
Due to their function, nerve fibers which carry afferent impulses are known as afferent nerves or sensory nerves, and those nerve fibers which carry efferent impulses are known as efferent nerves or motor nerves. On the other hand, the neurons which connect sensory nerves and motor nerves are known as interneurons or association nerve cells (Fig. 1).

### General Description

Both afferent and efferent terms have been derived from French. Afferent from *ad ferens* (Latin *ad* literally means **to** and verb *ferre* means **bring**) = **bring towards**, and efferent from *ex ferens* (Latin *ex* means **from** and verb *ferre* means **carry**) = **carrying away**.

The PNS gathers information from the environment and directs it towards the CNS; the CNS processes this information and directs it back to the PNS for suitable reaction. For example, when you accidentally touch a hot iron-press, the heat sensation is transmitted by the peripheral nerve to

**Afferent and Efferent Impulses, Fig. 1** Afferent and efferent nerve fiber (Image adapted from: <https://www.khanacademy.org/science/biology/human-biology/neuron-nervous-system/a/overview-of-neuron-structure-and-function>. This image is licensed under a CC BY-SA 4.0 license)



the spinal cord (afferent impulse), upon which spinal cord sends back signals through the nerves to the limb to initiate some motor action like to withdraw your limb or to push away the iron-press (efferent impulse). (Ganong, 2005) In former case, sensory neurons are involved; whereas in latter case, motor neurons execute the desired actions. The sensory neurons receive a wide variety of stimuli such as taste, smell, light, pain, etc. through different senses and sends these signals upwards through the nerves to reach in the CNS. Hence, these are also known as afferent or ascending pathways. The motor neurons form the efferent or descending pathways as they pass the signals along the nerves to the effector organ, which are primarily the muscles and glands (Fig. 1).

As evident from fig. 1, there is structural difference between afferent and efferent neurons. Afferent impulses are transmitted by pseudo-unipolar nerve cell, that is, it contains a soma with long axon that splits into two branches; one branch runs to the periphery and the other toward the spinal cord. Therefore, no dendrites are present in this case. The soma of efferent neuron is satellite shaped and consists of several shorter

dendrites projecting out of it along with a long axon. This axon generally forms a neuromuscular junction with the effectors. (Dharani, 2015) The motor neuron is present in the grey matter of the spinal cord and medulla oblongata and forms an electrochemical pathway to the effector organ or muscle.

## Cross-References

- ▶ [Action Potentials](#)
- ▶ [Axon](#)
- ▶ [Nerve Cells](#)
- ▶ [Neural Impulse](#)
- ▶ [Neuron](#)

## References

- Baars, B. J., & Gage, N. M. (2010). Neurons and their connections. In *Cognition, brain, and consciousness* (pp. 69–71). Burlington: Academic.
- Dharani, K. (2015). Physiology of the neuron. In *The biology of thought* (pp. 31–35). Chennai: Academic.
- Ganong, W. F. (2005). Reflexes. In *Review of medical physiology* (pp. 129–130). Singapore: McGraw Hill.

# D

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## Dopamine Receptor

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### Synonyms

DRD

### Definition

A class of G-protein-coupled receptors whose endogenous agonist is the neurotransmitter dopamine.

### Introduction

The neurotransmitter dopamine plays a significant role in influencing locomotor activity, attention, motivation, positive reinforcement, cognitive functions, and hormonal regulation as it interacts with a family of G-protein-coupled receptors. The main dopamine systems arise from the midbrain and the hypothalamus. Dysregulation of dopamine is suggested to be at the root of a number of major neuropsychiatric disorders (Daly and Salloway 1994).

## The Dopamine System

The cells of the midbrain that involve dopamine can be divided into the three groups: A8 in the retrorubral field, A9 in the substantia nigra, and A10 in the ventral tegmental area. Neurons found in the retrorubral field and the substantia nigra ascend to the striatum to form sections of the extrapyramidal system, a network that governs and coordinates involuntary movement. Neurons in the ventral tegmental area project to the limbic and cortical areas, forming the mesolimbic and mesocortical tracts. These neurons may be involved in emotional expression and cognitive functioning (Daly and Salloway 1994).

### Subtypes

There are five different types of dopamine receptors, divided into two classes, activation (D1 and D5) or reduction (D2, D3, and D4) of cyclic AMP (adenosine 3':5'-monophosphate; cAMP) (Binder et al. 2009). cAMP, or cyclic AMP, is an intracellular second messenger generated by adenylyl cyclase and deriving from ATP (Offermanns and Rosenthal 2008).

### D1-like Family (Activation)

#### D1

Dopamine receptor D1 is by far the most abundant subtype in the brain, found in elevated

concentrations in the substantia nigra pars reticulata, the caudate, the putamen, the nucleus accumbens, the olfactory tubercle, and both the front and temporal lobes (Daly and Salloway 1994). It is encoded by the DRD1 gene and is found postsynaptically on such dopamine-receptive cells as the GABA-ergic medium spiny neurons (MSNs) in the striatum (Beaulieu and Gainetdinov 2011). D1 receptor activation on postsynaptic neurons is especially associated with a stimulatory effect on locomotor activity. As a whole, D1 receptors regulate neuronal growth and development, mediate some behaviors, including reward, and also modulate D2 receptor-related events (The National Center for Biotechnology Information 2017).

#### D5

The roles of the D5 receptors remain less clear than the roles of the D1 and D2 receptors. However, the D5 receptors can be found at low levels in a variety of brain regions, including the pyramidal neurons of the prefrontal cortex, the premotor cortex, the cingulate cortex, the entorhinal cortex, substantia nigra, hypothalamus, the hippocampus, and the dentate gyrus. A very low level of expression has also been observed in the MSNs of the caudate nucleus and nucleus accumbens. It is thought that D5 might have some slight control over movement, and even possible control over cognitive functioning that involves the hippocampal regions (Beaulieu and Gainetdinov 2011).

#### D2-like Family (Reduction)

##### D2

Along with D3 receptors, D2 receptors are expressed both postsynaptically on dopamine target cells and presynaptically on the dopaminergic neurons. At its highest levels, D2 receptors are found most in the striatum, the nucleus accumbens, and the olfactory tubercle. Additionally, they are found in significant quantities in the substantia nigra, the ventral tegmental area, the hypothalamus, the cortical areas, the septum, the amygdala, and the hippocampus (Beaulieu and Gainetdinov 2011). D2 is also expressed in the retina and the kidney.

D2 receptors play a role in a number of bodily processes, including locomotor activity. Activation of the D2-like family of autoreceptors on the presynapse causes a decrease in dopamine release that reduces locomotor activity, whereas a corresponding activation on the postsynapse leads to the stimulation of locomotor activity. D2 receptors appear to be heavily involved in the presynaptic regulation of the firing rate, synthesis, and release of dopamine (Beaulieu and Gainetdinov 2011). Importantly, the two splice variants of D2 receptors, D2S and D2L (“Short” and “Long” respectively), have differing neuronal distributions: D2S is largely found presynaptically, while D2L is mainly postsynaptic. D2, in tandem with D1, is responsible for learning and memory functions, as related to the prefrontal cortex. D2 receptors also mediate prolactin secretion as well as take on a variety of other roles outside the central nervous system (Beaulieu and Gainetdinov 2011).

##### D3

Receptor D3 is similar yet distinct from D2 in that it is only a presynaptic receptor. It is found in the olfactory tubercle, the nucleus accumbens, the striatum, the substantia nigra, and the hypothalamus, and may in fact play the role of an “autoreceptor” as suggested by its presynaptic location and high affinity for dopamine. It can then be said that D3 may monitor the amount of synaptic dopamine in the brain (Daly and Salloway 1994).

D3 receptors are also found in the islands of Calleja, in the temporal lobe of the brain. Due to their mentioned role as autoreceptors, it seems that D3 moderately inhibits locomotor activity and, moreover, may be involved in cognitive functions that are mediated by the hippocampal regions, just as has been found with D5 (Beaulieu and Gainetdinov 2011).

##### D4

The D4 receptor is distributed across the frontal cortex, the medulla, the hypothalamus, and to a lesser degree across the basal ganglia (Daly and Salloway 1994).

D4 has the least amount of expression of all the receptors. Like D5, D4 has only a minimal

influence on movement, and like D3, it may play a role in the cognitive functioning mediated by the hippocampus. Along with both D3 and D5, the physiological role of D4 remains rather unclear (Beaulieu and Gainetdinov 2011).

## Links to Pathology

### Attention-Deficit-Hyperactivity Disorder

It is hypothesized that people with Attention-Deficit-Hyperactivity Disorder (ADHD) may have inefficiency in processing dopamine in the frontal lobes and within the frontostriatal neuronal circuitry to such an extent that a significant amount of dopamine is removed from their brain by way of a high instance of dopamine transporter levels (Ferrell 2010; Hedlund 2013). This seems to play a role in causing the hallmark symptoms of impulsivity, hyperactivity, and inattention (Ferrell 2010). Dopamine receptors D4 and D5 have been especially implicated in this pathological process (Miller 2011).

### Substance Abuse and Addiction

The mechanisms behind the action of drugs such as cocaine, amphetamines, and nicotine have been said to involve dopamine (Bough et al. 2015).

Cocaine binds to the dopamine transporter and blocks its functioning, causing dopamine to accumulate within the synaptic cleft. This results in extended and enhanced dopamine signaling. After sustained cocaine use, decreased dopaminergic signaling may be the culprit in depressed mood disorders and the sensitization of the meso-dopaminergic circuit toward cocaine's reinforcement, leading to dependency (Bough et al. 2015).

Amphetamines cause the release of dopamine from the mesocorticolimbic system and the nigrostriatal neurons, inhibiting some metabolic enzymes and acting as a direct agonist on serotonin receptors (Bough et al. 2015).

Nicotine consumption, such as through tobacco use, increases dopamine levels and stimulates the reward and pleasure pathways as nicotine receptors bind to the brain. After long-term exposure to nicotine, addiction may become an issue (Bough et al. 2015).

### Schizophrenia

Schizophrenia is a severe mental illness, notable especially for its psychotic symptoms, diminished affect, and cognitive abilities. The dopamine hypothesis as proposed by Arvid Carlsson in 1963, which states that elevated dopamine transmission contributes to schizophrenia's symptoms, is still well-regarded today and came about through experimentation with first-generation antipsychotics. More modern revisions to the hypothesis have specified locations of hyperactive dopamine transmission in the mesolimbic areas and prefrontal cortex, as well as the amygdala (Brisch et al. 2014).

A decrease of D1 receptors in the prefrontal cortex is seen in schizophrenia patients, which contrasts with the elevated expression of D1 in the parietotemporal cortex. A significant increase of D2 in the striatum of schizophrenia patients has been noted as well. The decrease of D2 in the thalamus and anterior cingulate cortex may point to abnormalities in transmission from these regions to the prefrontal cortex. Both types of neuroleptics, typical and atypical, increase the expression of high-affinity D2 receptors, as do dopamine antagonists and agonists. High-affinity D2 expression in large amounts has been seen as an indicator for psychosis. In this way, antipsychotic treatment may be seen to fail in some patients because it elevates this sort of D2 expression that is associated with the increase of psychotic symptoms themselves (Brisch et al. 2014).

It is clear that every effective neuroleptic that has been formulated has had some connection to the neurotransmitter dopamine as it interacts with other neurochemicals such as glutamate, GABA, serotonin, and acetylcholine (Brisch et al. 2014).

### Parkinson's Disease

Parkinson's is primarily considered a neurodegenerative movement disorder as it involves resting tremors, rigidity, postural instability, and freezing, among such other complications as depression, sleep disturbance, and dementia, the last one occurring especially in the late stages. Dopamine is thought to be at the root of this symptomatology, though the disease affects multiple systems (Prediger et al. 2014). The degeneration of

dopaminergic neurons in midbrain nigrostriatal pathway, and thus the decline of midbrain dopamine transmission, has been pointed out as a particular focal point of the disease's etiology (Prediger et al. 2014; Double and Finberg 2016). The work of Arvid Carlsson and the prescription of L-Dopa, a medication that elevates dopamine levels, contributed greatly to the advancement of knowledge on the neurobiology behind Parkinson's (Double and Finberg 2016). Agonistic activity on D2 receptors through medication contributes to the reduction of Parkinson's symptoms, but may lead to side effects such as the vomiting, hallucinations, and hypotension associated with elevated dopamine levels (Prediger et al. 2014).

## Dopamine and the Animal Kingdom

Dopamine controls locomotor activity in animals and other vertebrates just as it does in humans. Additionally, the reward mechanism that involves dopamine has been identified through single-cell recording of dopamine neurons in animals, and dopamine has been implicated in the biology of depression in animals. However, dopamine's role in depression has been found less in humans (Blanco 2017). It is with studies involving D2 receptor-deficient mice that dopamine involvement in locomotion and reward systems has been substantiated (Oak and Van Tol 2008).

In speaking about the confluence of dopamine, animals, and reward, it is important to mention temporal difference learning. Temporal difference learning is a reinforcement-learning algorithm that learns to predict future rewards through a reward-prediction error signal, and is especially used as both a model for animal learning and dopamine activity (Seel 2012). The algorithm is an estimation tool in a way, in that it compares the prediction of a future reward to the observed reward and the estimated value of the next state. In a series of important studies, Wolfram Schultz and his colleagues found that during classical conditioning with monkeys, dopamine neuron firing corresponded strongly with the temporal difference learning model in that dopamine neurons

fired to unexpected rewards that have no precedent. This is due to a significant prediction error, as expressed by temporal difference algorithm. Dopamine neurons stopped firing after exposure to a consistent reward as suggested by the model, i.e., when subjects' predictions matched reward outcome. The temporal difference model is the dominant theory of the dopamine response to learning and has since been suggested as the basis for other models of learning beyond classical conditioning. Investigation has branched out to other subject models, including humans and rats, and other fields beyond reinforcement learning, including the burgeoning realm of neuroeconomics. The outlook is bright for further studies on this topic (Ludvig 2012).

Mice lacking in dopamine transporter show signs of hyperactivity, possibly due to a hyperdopaminergic state, and animals deficient in D2 receptors show dopamine autoreceptor-mediated cell firing inhibition (Harsing 2008). The dopamine overflow, caused by the stimulant methylphenidate, that leads to greater potentiation in dopaminergic drugs was first demonstrated in animal testing (Harsing 2008).

## Cross-References

- ▶ [ADHD](#)
- ▶ [Hippocampus](#)
- ▶ [Hypothalamus](#)
- ▶ [Locomotion](#)
- ▶ [Medial Prefrontal Cortex](#)
- ▶ [Medial Striatum](#)
- ▶ [Neuron](#)
- ▶ [Neurotransmitters](#)
- ▶ [Nucleus Accumbens](#)
- ▶ [Parkinson's Disease](#)

## References

- Beaulieu, J., & Gainetdinov, R. R. (2011). The physiology, signaling, and pharmacology of dopamine receptors. *Pharmacological Reviews*, 63(1), 182–217.
- Binder, M. D., Hirokawa, N., & Windhorst, U. (2009). Dopamine receptors. In *Encyclopedia of neuroscience* (p. 995). New York: Springer.



- Blanco, N. J. (2017). Dopamine. In V. Zeigler-Hill & T. K. Shackelford (Eds.), *Encyclopedia of personality and individual differences* (pp. 1–4). Cham: Springer.
- Bough, K. J., Khalsa, J. H., & Gyaw, S. (2015). Neurobiological complications of substance abuse. In N. El-Guebaly, G. Carrà, & M. Galanter (Eds.), *Textbook of addiction treatment: International perspectives* (pp. 1669–1692). Milan: Springer.
- Brisch, R., Saniotis, A., Wolf, R., Biela, H., Bernstein, H.-G., Steiner, J., et al. (2014). The role of dopamine in schizophrenia from a neurobiological and evolutionary perspective: Old fashioned, but still in vogue. *Frontiers in Psychiatry*, 5, 47.
- Daly, J. M., & Salloway, S. (1994). Dopamine receptors in the human brain. Retrieved 20 Jan 2017, from Psychiatric Times, <http://www.psychiatrictimes.com/neuro-psychiatry/dopamine-receptors-human-brain>
- Double, K., & Finberg, J. (2016). Parkinson's disease. In D. W. Pfaff & N. D. Volkow (Eds.), *Neuroscience in the 21st century* (Vol. XXI, pp. 3843–3861). New York: Springer.
- Ferrell, C. B. (2010). Attention deficit/hyperactivity disorder (ADHD). In C. S. Clauss-Ehlers (Ed.), *Encyclopedia of cross-cultural school psychology* (pp. 132–135). New York: Springer.
- Harsing Jr., L. G. (2008). Dopamine and the dopaminergic systems of the brain. In A. Lajtha & E. S. Vizi (Eds.), *Handbook of neurochemistry and molecular neurobiology* (pp. 149–170). New York: Springer.
- Hedlund, G. L. (2013). Children with attention-deficit-hyperactivity disorder (ADHD): Evidence-based neuroimaging. In L. S. Medina, P. C. Sanelli, & J. G. Jarvik (Eds.), *Evidence-based neuroimaging diagnosis and treatment* (pp. 299–306). New York: Springer.
- Ludvig, E. A. (2012). Reinforcement learning in animals. In N. M. Seel (Ed.), *Reinforcement learning in animals* (pp. 2799–2802). New York: Springer.
- Miller, C. J. (2011). Attention deficit hyperactivity disorder (ADHD). In R. J. Levesque (Ed.), *Encyclopedia of adolescence* (pp. 211–225). New York: Springer.
- Oak, J. N., & Van Tol, H. H. (2008). Dopamine system. In S. Offermanns & W. Rosenthal (Eds.), *Encyclopedia of molecular pharmacology* (pp. 437–442). Berlin/Heidelberg: Springer.
- Offermanns, S., & Rosenthal, W. (2008). *Encyclopedic reference of molecular pharmacology*. Berlin/Heidelberg: Springer/GmbH.
- Prediger, R. D., Bortolanza, M., Carolina de Castro Issy, A., Lopes dos Santos, B., Del Bel, E., & Raisman-Vozari, R. (2014). Dopaminergic neurons in Parkinson's disease. In R. M. Kostrzewa (Ed.), *Handbook of neurotoxicity* (pp. 753–788). New York: Springer.
- Seel, N. M. (2012). Temporal-difference learning. In *Encyclopedia of the sciences of learning* (p. 3303). New York: Springer.
- The National Center for Biotechnology Information. (2017). *DRD1 dopamine receptor D1 [Homo sapiens (human)]*. Retrieved from <https://www.ncbi.nlm.nih.gov/gene/1812>

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# G

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## Gestalt

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### Synonyms

[Configurational processes](#); [Gestalt laws](#); [Perception](#); [Perceptual figures](#); [Whole](#)

### Definition

Gestalt psychology was a school of thought originating in the early twentieth century that defended a molar view of perception. According to Gestalt principles, perception involves an active organization of stimuli that takes place within schemes of meanings. A widespread contribution of gestalt theory was to synthesize in laws the ways in which perceptual information tends to be grouped through conceptualization.

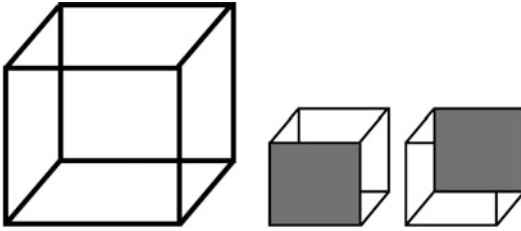
### Introduction

Essentially, Gestalt psychology defined perception as a process that organized the world of objects. According to gestalt theorists, this process is led by meanings and not by the adding of one part to others. The objective of gestalt

principles was to demonstrate that perception is not simply an accumulation of information.

If we search the etymological sense of the term, Gestalt is a German noun that means form, or figure. Additionally, Gestalten is a verb that means organize, configure, or restructure. Gestalt psychology postulates an innate origin of certain categories that give rise to the schemas in which we perceive. The theory claims that perception does not come from emptiness but, as Kant stated (Oviedo 2004), perception goes beyond the literal data and builds global phenomena. Classic examples of gestalt perception include well-known optical illusions in which a visual pattern can be perceived according to multiple conceptualizations. An example of this is the Necker cube (see Fig. 1), in which two different cubes may be perceived, depending on the point where the deeper perspective is fixated. To gestalt theorists, this is proof that a molecular definition of perception is not possible. That is, the object perceived comes from a qualitative organization of stimulus characteristics. Depending on the frame of perception, object perception can change without modifying the composition or arrangement of its features. Another well-known example, characteristic of gestalt analysis, is the image of the young and the older woman and its numerous versions (see Fig. 2).

In contrast to the atomistic perspective of cognition, which claims additive summation of discrete stimuli as the main function of perception (Katz 1945), Gestalt psychology suggests that



**Gestalt, Fig. 1** Necker cube. The perspective of the 3D cube can change depending on the fixation point



**Gestalt, Fig. 2** Older and young women illusion (Adapted from Boring 1930)

perception involves forming hypotheses about stimuli in the world. Historically, taking into account the physiological trends up until the early twentieth century, Gestalt explanations in terms of meanings, wholes, and interpretations of stimuli seemed revolutionary. The Gestalt theory contrasted with the historical period in which it emerged because of its molar level of explanation, in opposition with the elementary point of view. For instance, Katz (1945) supports the idea that an atomistic perspective of perception cannot explain rhythmic auditory stimulation and, consequently, the melodic music experience as a perceptual phenomenon. Katz says, that in a succession of metronome oscillations, different rhythm patterns can be heard depending the speed of the beat. For this author, the dynamic organization of auditory figures is essential for the experience of rhythm.

This molar view of the act of perception fits with the existence of perceptual constancies. Perceptual constancy is an invariance of meaning within a given perceptual category. Even if one discrete characteristic of a target varies, our recognition of the target category does not vary. For example, viewpoint invariance (Goldstein 2010) is the ability to visually recognize a known object, despite it being presented from different angles. Another perceptual constancy is size, seen in the capacity to recognize a moving object although it is displayed in different sizes because of changes in distance. Color constancy is another basic constancy that brings simplicity to the multiple and variable stimulus world in which we live. Color constancy brings the possibility to group different palettes of tonality (turquoise, indigo, cobalt, sapphire, azure), as the same color, blue. From a gestalt view, the whole remains separate from its specific parts.

In short, the core of Gestalt theory may be summarized by the classic slogan, “the whole is greater than the sum of its parts” (Boring 1929, pp. 588–589). This whole may be observed in everyday examples such as perception of auditory melodies, in which notes sound different in the context of the melody than if they are heard in isolation. In taste perception, the combination of several flavors results in a totally different whole than the isolated ingredients. In this regard, another example widely explored in animal learning is the taste flavor paradigm. It is a well-known phenomenon in which a two-flavor compound tastes qualitatively different from each component tasted separately (Rescorla and Cunningham 1978).

Besides the aforementioned ideas, the Gestalt perspective introduced inference into the perception process. Perception is the act of grouping the myriad stimuli in the environment into dynamic wholes (Ellis 1938). For the Gestalt psychologist, perceivers are active organizers of stimuli. Gestalt psychology defended the experimental study of perception as a flexible status to fit and adapt to the environment, working between exteroception, interoception, and cognition in an organizational way.

The basic topics of gestalt theory (Boring 1929) include the study of principles of relativity and transposition, related with generalization and discrimination processes in different perceptual variables. In this case, differentiating indigo from other blue tonalities is a discrimination exercise. Conversely, deciding that turquoise is also blue is an example of generalization. Additionally, in early Gestalt works, other principles to explore were the underpinnings of object constancy, field dynamics, and laws of form.

The rest of the entry is divided into three sections. The first is a historical overview of the principal authors from Gestalt psychology. The second is an exposition and synthesis of the Gestalt laws. Although the majority of the examples in the literature are on visual reorganization, gestalt laws may be observed in all perceptual modalities. Thus, perception is to see, hear, touch, smell, or taste from a scheme of meaningful organization. An assortment of examples will illustrate these principles. In the third and final section, the relationship between gestalt theory and general cognition will be discussed.

## Origins of Gestalt Theory

Gestalt psychology was developed primarily by Max Wertheimer, Wolfgang Köhler, and Kurt Koffka, in the first decades of the twentieth century. These authors were German psychologists who began their careers together at the Berlin Psychological Institute.

Max Wertheimer (1880–1943) published what many consider to be the first work of Gestalt psychology in his 1912 paper on the *phi* phenomenon (Wertheimer 1912). In this phenomenon, participants perceive illusory motion when they are presented with a sequence of spatially displaced images (Wagemans et al. 2012). In the original procedure, participants were exposed briefly to a line, followed by a short delay, and then by a second line, parallel to the first, and spatially separated. When the delay was below a certain threshold (about 30 ms), participants perceived only one, stationary line; when the delay was above a certain threshold (about 200 ms),

participants correctly perceived two lines, one appearing after the other; however, when the delay was at a certain middle value (about 60 ms), participants perceived a single line in motion. This final illusory motion effect is the same one that underlies our perception of motion in films, which consist of a series of static images. Wertheimer concluded that motion perception emerged as a perceptual whole, or *gestalt*, that was qualitatively different from any of its separate elements. This finding thus served as a starting point for the development of Gestalt theory (Wagemans et al. 2012).

Wolfgang Köhler's most essential findings came from his experiments on chimpanzee intelligence, published in *The Mentality of Apes* (Köhler 1925). In these experiments, Köhler (1887–1967) set out to test the extent to which chimpanzees could manipulate the environment or use tools to obtain food that was out of reach. For instance, in one experiment, a basket of fruit was hung in the air, with some boxes placed on the ground off to the side. The only way for the chimps to reach the fruit was to stack the boxes on top of each other underneath the fruit basket and climb them. Some of the chimpanzees tested (although not all) in fact did this. In another experiment, the only tools available to the chimpanzees were a pair of short sticks that they needed to insert into each other to create a longer stick able to reach the fruit basket and knock it over. One chimpanzee in fact did this. In another experiment, the only solution was to use a short stick to reach a longer stick and then use the longer stick to knock over the fruit basket. Several of the chimpanzees were able to solve the task.

Importantly, in all these experiments, the chimpanzees received no explicit training with the tools involved. Rather, it appeared that they came upon the solution through what Köhler called insight: a mental process in which the elements in the environment came to be perceived in relation to each other as a unique stimulus whole that made the solution obvious, as in an “aha” effect. Köhler described that, when faced with each problem, the chimpanzees initially tried to reach the food directly with their hands, but eventually gave up that futile approach and appeared to

**Gestalt, Fig. 3** Example of organization



sit in thought for a while, examining the surroundings. The chimpanzees' attention eventually focused upon the available tools and, a few moments later, the chimps proceeded to use the tools more or less correctly for the purpose of obtaining the food. Köhler argued the core of this insight process was the perception of the complete environment and all of its parts in relation to each other, and a reorganization of the stimulus elements in the chimpanzee's mind to achieve a new perception that was qualitatively different from the sum of its separate parts. Köhler viewed this type of learning as fundamentally different from the mechanistic S-R learning proposed by another prominent psychologist of the time, Edward Thorndike (Ruiz and Sánchez 2014), whose theory might predict that the chimpanzees would arrive at the solutions only gradually and through trial and error. Köhler observed quite the opposite: that the solution appeared rather swiftly after a careful reflection of the situation.

Kurt Koffka (1886–1941) contributed to the development of Gestalt theory with the publication of works such as *Principles of Gestalt Psychology* (1969). As Goodwin (1999) recalled, Koffka did his PhD in Berlin exploring perceptual contrast of color and the study of rhythm in auditory stimuli (Goodwin 1999). Koffka also got involved in Wertheimer's apparent motion experiments, as did Köhler. His work built upon that of Wertheimer and Kohler and applied it to new areas such as child development. Like his colleagues, Koffka also sought to distinguish gestalt theory from the prevailing behaviorist theory of the time. He argued that while behaviorists, such as Thorndike, refused to study conscious mental phenomena, gestalt theory tackled these phenomena directly and successfully. Furthermore, Koffka spent the later part of his career as

a professor in American universities such as Cornell, the University of Wisconsin, and Smith College, and as such was the main promoter of the Gestalt perspective in America.

### Gestalt Laws of Form

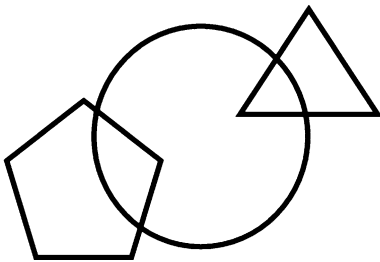
Besides explaining perception in terms of schemas of meaning, Gestalt psychology formulated the Laws of Gestalt. These laws summarized the general trends of how we organize our perceptual world. First studied by Wertheimer between 1923 and 1967 (Goodwin 1999), Gestalt laws assumed that elements are organized as part of a meaningful whole. This organizational principle underscores the ultimate purpose of the perceptual process, to find meaning in the chaotic world of stimuli that surrounds us. Each law exposed below organizes figures through a common purpose, soft lines, symmetrical order, space distribution, similar features, or same orientation. Gestalt organization also tends to the maximum simplicity that encourages the maximum effectiveness of perceptual effort. For instance, Fig. 3 shows a simple example of gestalt organization. A plain set of two points and a line are quickly organized as a schema of a human smiling face.

As Boring first claimed (1929), Gestalt principles form the basis for 114 laws of perception. However, the main rules that appear in basic perception manuals can be grouped as follows.

1. **Good Form or Pregnancy.** This law, also known as Common Destiny or Simplicity, was formulated by Koffka (1969). This law states that elements that share a common end, following the simplest principle, tend to be considered as being from the same figure. A common end could be a meaningful category or schema. This rule helps the perceiver to differentiate parts from different objects that visually overlap with each other (Katz 1945), as Fig. 4 shows. It also operates when there are several options of figures in the perceptual field. The constellations in astronomy are pure examples of gestalt pregnancy. Figure 5 shows the basic stimulus input that comprises

the Ursa Major constellation and the schema that provides the image of a bear. Another interesting example in another sensory modality is the effect studied by Benussi (in Katz 1945). In this tactile effect, the stimulation provoked by three points of pressure in the skin, delimiting a triangle, is perceived as a circle sensation.

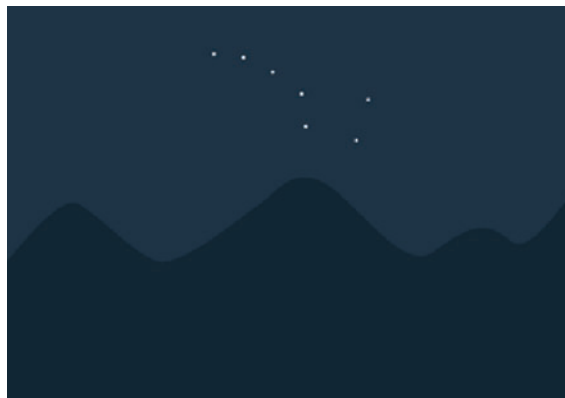
2. **Closure.** Human perception tries to complete or close figures (Katz 1945). People prefer closed to unclosed figures (Wertheimer 1923). This tendency to complete incomplete sensorial information takes place in an automatic way. All the information provided to help to finish a contour will be selected to outline a whole, as Kanizsa showed in his varied incomplete triangles and other invisible border images (1976). A proof can be seen by removing a part of any geometric shape, a



**Gestalt, Fig. 4** Delimitation of geometric figures from Good Form law. Example of delimitation of edges following the geometric schemas of pentagon, circle

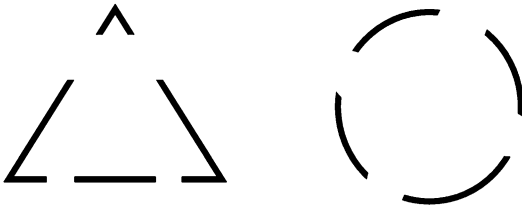
triangle for example. In Fig. 6, one can observe the difficulty of ignoring the whole shape despite being incomplete. An example from the auditory domain is known as auditory closure strength, the ability to listen to the whole message in a radiophone speech with interference (Katz 1945). An example of the same phenomenon in a visual-reading domain can be seen in Fig. 7.

3. **Continuity or Good Continuation.** Human perception tends to complete lines but also softly, and tends toward the circle shape (Wertheimer 1923). For example, motor integration involves a preference for indirect and circular movements in the perception of human motor translation. In Fig. 8, one can see a clear example of continuity in which the viewer tends to perceive two softly curved lines, rather than pointy shapes. In another example, from ethology, there is a preference for soft and circular shapes in mammalian offspring. Lorenz (1943) showed that similarities exist in some physical characteristics of young animals, such as round faces. Maps also can be a good model of continuity; we are able to distinguish geographic delimitations from many overlapping lines.
4. **Symmetry.** Figures are usually perceived as symmetrical. Asymmetries tend to be neutralized (Katz 1945). This principle completes and emphasizes the aforementioned rules and shows a perceptual preference for



**Gestalt, Fig. 5** Draw Illustration of Ursa Major. Exemplification of Gestalt Pregnancy. A bear figure can be perceived from a few spots in the sky. (From: Pixabay)





**Gestalt, Fig. 6** Examples of geometric closure. Triangle and circle are visible for the closure gestalt law

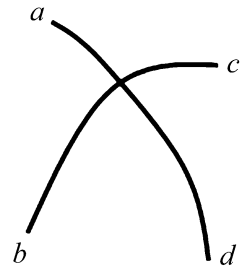
# gestalt

**Gestalt, Fig. 7** Example of Closure in reading

homogenous images and sensorial perceptions. Also, the objects that tend to be symmetrical, that is, those equally distributed around their axis, are easily perceived and selected.

5. **Proximity.** Stimuli near each other tend to form a unity (Wertheimer 1923). Good examples of this are from auditory perception of musical patterns. A piece played slowly, or “lento” in musical terms, can hardly be heard as the same piece when it is performed quickly, or “presto.” Another auditory phenomenon is that of auditory segregation, which is similar to the proximity effect (Bregman and Campbell 1971). In the original experiments, these authors presented an alternating sound sequence of low (between 350 and 550 Hz) and high tones (between 2500 and 1600 Hz). When the sequence was played slowly (interstimulus-interval of 400 ms), a pattern of successive low and high stimuli clearly appeared. When the same sequence was presented faster (interstimulus-interval of 100 ms), the perception was divided into two auditory paths: a high one and a low one. This segregation effect, due to temporal proximity between similar sounds, can be experienced in the classical music opus S. 141 study of Litz, commonly known as “Campanella.” In Fig. 9, one can also see a visual example. The

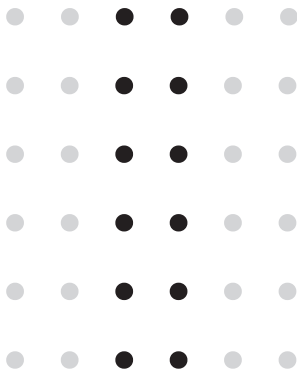
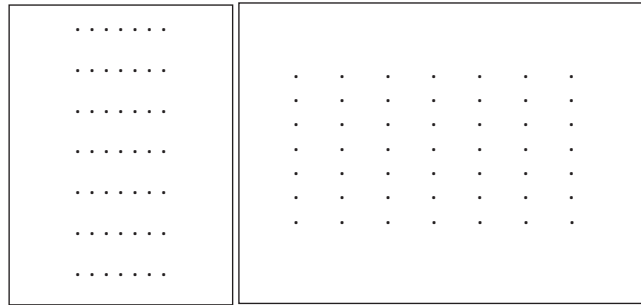
**Gestalt, Fig. 8** Example of Good Continuation. Facing the task of determining the start and end of those two lines, Good Continuation predicts the limits of one from *a* to *d*, and the other from *b* to *c*, due to a preference for soft lines over sharp corners. The scheme of letter *x* in the Western alphabet may also be influencing (Adapted from Katz 1945)



elements in each set of points are the same, but they differ in its spatial distribution, creating a very different visual result.

6. **Similarity.** Stimuli that share features tend to form a unity. Lightness, color, texture, size, shape, (Goldstein 2010) are possible characteristics to be grouped, as can be seen in Fig. 10. In a complex visual pattern, as a Monet painting, the figures can emerge from the similarity of color, size, and texture of the brush strokes, as can be seen in his studies of “Water Lilies.” The similarity principle is evident in the painting style of lots of impressionistic artists. Moreover, a painting technique called pointillism uses similarity and gestalt principles, using the different color points to conform the scenes, as Van Gogh and Seurat did.
7. **Good direction or Common fate.** This principle takes into account the movement or tendency to group elements in the same direction (Wertheimer 1923). Orientation and synchronicity in the static figures is relevant to define figures. In Escher’s paintings, common fate is a clue to discern the different illusions hidden in each drawing, like in his series “Sky and Water.”
8. **Strong form.** A strong or intense stimulus tends to be differentiated from other stimuli. If a strong stimulus competes with a weak stimulus, the strong stimulus tends to attract more attention. This is the case of the reorganization process called reification, the ability to see more information than is actually provided by the physical stimuli. The subject

**Gestalt, Fig. 9** Example of proximity. The same stimuli form different configurations (horizontal or vertical, respectively) depending on a proximal variable

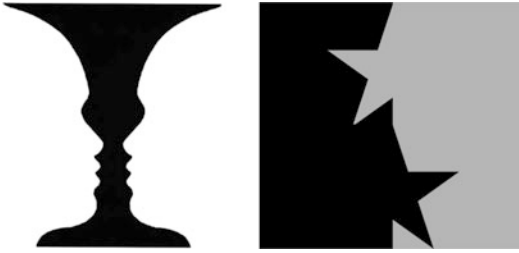


**Gestalt, Fig. 10** Similarity example. Columns of points tends to be grouped by shade identity

gives additional attributes in order to organize intense meanings. This reification process is governed by powerful meaning. Something similar happens in the pareidolia phenomenon. This cognitive process occurs when perceivers are able to distinguish concrete forms in a simple environment, like an artificial apparatus or a natural phenomenon. An example of this is the common example of seeing animals, faces, and other significant figures in the clouds. Something relevant in all these processes is considering that human faces are strong stimuli for human perception. This principle is reflected in the perception of a facial expression in Fig. 3. Similarly, in Fig. 2, one image is usually more difficult to see than the other. Sometimes, familiarity gives the stronger value to one option over another. This principle supports the next law to be considered in terms of differentiating strong figures from weak ones, which sometimes can be considered as background.

9. **Figure and Ground.** Human perception tends to fixate on one main point over the background. The figure has a defined outline that stands out from the ground. This principle explains why perceivers need a certain contrast to distinguish figures (Oviedo 2004). The first description of this principle was by Rubin (1921) and was illustrated by the classic faces and cup image, as can be observed in Fig. 11. Another example of the influence of ground in the perception of a figure is the visual differences depending on the color of possible backgrounds (see Fig. 11). Also, in Fig. 2, the hidden figure can be conceptualized as ground, since it is not possible to perceive both women at the same time. Koffka (1969) exposed an analysis of characteristics in which figure and ground are related, including factors such balance in color, limits of the figure contour, orientation, relative size, and feature complexity. In another perceptual paradigm, Signal Detection Theory (Green and Swets 1966) has widely developed the task of finding a figure (a Signal, in the terms of the theory) from the Ground (Noise, in the parlance of the theory). The particularity of this theory is the systematic study of different ambiguity conditions of figure and ground. Signal Detection methodology explores the measures of probability to perceive and decide between response or no response to the signals and possible false alarms that can be confounded with the ground.

10. **Stability.** When organizations are established, they are also difficult to eliminate and tend to persist. Gestalt perception tries to



**Gestalt, Fig. 11** On the *left* are the Rubin faces, a classic example of Figure and Ground. On the *right*, a combination of shades between Figure and Ground (Adapted from Rubin 1921)

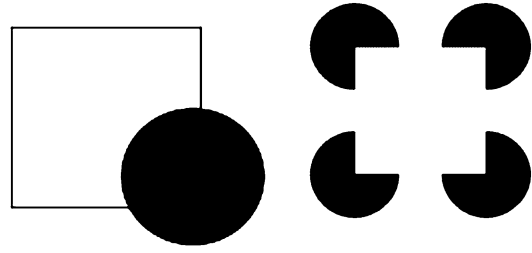
conform stable objects. For example, in visual illusions like the Necker cube (check Fig. 1) and the younger and older woman (see Fig. 2), the option not seen at first sight, is usually more difficult to see.

From all these laws, Closure, Good Continuation, Proximity, Similarity, and Figure and Ground are the most general and commonly observed. In lots of everyday examples, various laws work together. Several applied fields have explored the extent of these principles, with logos and advertisements serving as good examples of this. Also, analysis of visual art has made a lot of effort to apply gestalt principles to art perception.

## Gestalt Perception Theory and Learning

Gestalt principles have served as a platform for studying animal learning and cognition in a variety of contemporary research. One manner in which this has been done is through the study of perceptual laws outlined above, in animals. Studies of the perceptual constancies have been performed in species as diverse as parrots (Pepperberg and Nakayama 2016), ants (Sakiyama and Gunji 2016), mice (Kanizsa et al. 1993), and chimpanzees (Hopkins and Washburn 2002).

For instance, Pepperberg and Nakayama (2016) tested, in a parrot, the phenomena of amodal and modal completion. Amodal completion is the recognition of an object that is partially

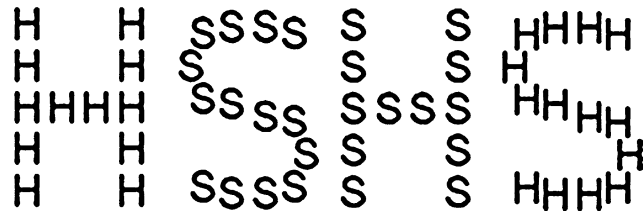


**Gestalt, Fig. 12** On the *left*, a square requiring amodal completion; on the *right*, a square requiring modal completion

covered, such as the square in Fig. 12a. Modal completion is the recognition of an object that lacks some of its boundaries, such as the square in Fig. 12b. Notice that the phenomena rely on the gestalt principles of good form and closure. Pepperberg and Nakayama tested whether a parrot could identify incomplete two-dimensional (2D) shapes similar to the ones in Fig. 6 after having been trained to verbally identify the corresponding three-dimensional (3D) shapes. They found that the parrot was indeed able to identify the incomplete 2D shapes, whether they required amodal or modal completion. Importantly, the parrot had previously been trained only with 3D shapes, and had never been tested with their 2D counterparts, let alone 2D shapes requiring completion. While the authors acknowledged that the exact mechanism underlying the results is not clear, the finding at least provides evidence that parrots might engage in a “gestalt”-style processing of the world, possibly reflecting higherorder cognitive abilities.

Another aspect of modern learning and cognition that draws a parallel from Gestalt psychology is the concept of configural, as opposed to elemental, processing (Wasserman 1997). Elemental processing refers to a bottom-up processing of the individual parts of a stimulus set, whereas configural processing refers to processing the complete stimulus set as a whole, akin to a gestalt. For instance, suppose an animal is presented with a light and tone simultaneously, followed by food. Elemental processing would be said to take place if the animal forms two distinct associations, one between the light and food, and another between

**Gestalt, Fig. 13** Local and global processing



the tone and food. Configural processing would be said to take place if the animal forms a single association between the light-tone configuration and food. Some modern learning theories use the concept of configural learning (e.g., Pearce 1987), and a number of findings suggest that configural associations play a role in animal learning (for a review, see Pearce and Bouton 2001). Other research suggests animals may engage in both types of processing in varying degrees (Honey et al. 2014).

A related concept in modern learning and cognition drawing inspiration from Gestalt psychology is that of global, as opposed to local, processing (Navon 1977). For instance, imagine one is asked to discriminate between hierarchical stimuli, such as those shown in Fig. 13, involving large letters made up of small letters. Local processing would be defined as focusing attention on the small letters, while global processing would involve focusing attention on the large letters, as in “seeing the forest before the trees.” Hopkins and Washburn (2002) trained chimpanzees and rhesus monkeys on discriminations between hierarchical stimuli similar to those shown in Fig. 13. The authors found that while rhesus monkeys performed better when the discrimination was between the small letters (local processing), the chimpanzees performed better when the discrimination was between the large letters (global processing). The global processing exhibited by the chimpanzees may be interpreted as a gestalt processing of the whole stimulus. More generally, there appears to be a relationship between cognitive complexity and global processing (Neiworth et al. 2006). In a study that compared adult humans with children and adult tamarin monkeys, adult humans showed the strongest tendency towards global processing, while children and

adults tamarin monkeys showed similar, lower levels (Neiworth et al. 2006).

As the preceding findings show, Gestalt-inspired principles serve as a useful basis for studying animal learning and cognition, as well as for performing cross-species comparisons. The general presumption is that the level of gestalt processing reflects the level of cognitive complexity, although the specific underpinnings of such processing remain unclear.

## Conclusion

Gestalt psychology defined perception as an active way to organize the stimuli that surround us. From first decades of the twentieth century, the primary Gestalt authors (Wertheimer, Koffka, and Köhler) experimentally studied the principles and laws which describe the general trends of how we group sensorial information. The Gestalt perspective changed the general conceptualization of the study of cognition, emphasizing that molar processing in perception could influence other basic psychological processes.

## Cross-References

- ▶ [Categorization](#)
- ▶ [Cognition](#)
- ▶ [Configural Perception](#)
- ▶ [Figure-Ground](#)
- ▶ [Generalization](#)
- ▶ [Insight](#)
- ▶ [Kanizsa Illusion](#)
- ▶ [Pareidolia](#)
- ▶ [Psychophysics](#)
- ▶ [Sensory Processes and Perception](#)

## References

- Boring, E. G. (1929/1950). *A history of experimental psychology* (2nd ed.). New York: Appleton-Century-Crofts.
- Boring, E. G. (1930). A new ambiguous figure. *The American Journal of Psychology*, *42*, 444–445.
- Bregman, A. S., & Campbell, J. (1971). Primary auditory stream segregation and perception of order in rapid sequences of tones. *Journal of Experimental Psychology*, *89*(2), 244–249.
- Ellis, W. D. (Ed). (1938). *A source book of Gestalt psychology*. London: Kegan Paul, Trench, Trubner & Company.
- Goldstein, E. B. (2010). *Sensation and perception* (8th ed.). Belmont, CA: Wadsworth Cengage Learning.
- Goodwin, C. J. (1999). *A history of modern psychology*. Hoboken: Wiley.
- Green, D. M., & Swets, J. A. (1966). *Signal detection theory and psychophysics*. New York: Wiley.
- Honey, R. C., Iordanova, M. D., & Good, M. (2014). Associative structures in animal learning: Dissociating elemental and configural processes. *Neurobiology of Learning and Memory*, *108*, 96–103.
- Hopkins, W. D., & Washburn, D. A. (2002). Matching visual stimuli on the basis of global and local features by chimpanzees (*Pan troglodytes*) and rhesus monkeys (*Macaca mulatta*). *Animal Cognition*, *5*(1), 27–31.
- Kanizsa, G. (1976). Subjective contours. *Scientific American*, *234*(4), 48–52.
- Kanizsa, G., Renzi, P., Conte, S., Compostela, C., & Guerani, L. (1993). Amodal completion in mouse vision. *Perception*, *22*(6), 713–721.
- Katz, D. (1945/1944). *Psicología de la forma*. Madrid: Espasa Calpe. (First published as *Gestalt psychology*, Ed. Basel, B. Schwabe & Co.).
- Koffka, K. (1969/1935). *Principios de la psicología de la forma*. Buenos Aires: Paidós. (First published as *Principles of Gestalt psychology*, Ed. Routledge).
- Köhler, W. (1925). *The mentality of apes*. New York: Harcourt, Brace and Company Inc.
- Lorenz, K. (1943). Die angeborenen Formen moeglicher Erfahrung. *Zeitschrift für Tierpsychologie*, *5*, 235–409.
- Navon, D. (1977). Forest before trees: The precedence of global features in visual perception. *Cognitive Psychology*, *9*(3), 353–383.
- Neiworth, J. J., Gleichman, A. J., Olinick, A. S., & Lamp, K. E. (2006). Global and local processing in adult humans (*Homo sapiens*), 5-year-old children (*Homo sapiens*), and adult cotton-top tamarins (*Saguinus oedipus*). *Journal of Comparative Psychology*, *120*(4), 323.
- Oviedo, G. L. (2004). La definición del concepto de percepción en psicología con base en la psicología Gestalt. *Revista de Estudios Sociales*, *18*, 89–96.
- Pearce, J. M. (1987). A model of stimulus generalization for Pavlovian conditioning. *Psychological Review*, *94*, 61–73.
- Pearce, J. M., & Bouton, M. E. (2001). Theories of associative learning in animals. *Annual Review of Psychology*, *52*(1), 111–139.
- Pepperberg, I. M., & Nakayama, K. (2016). Robust representation of shape in a Grey parrot (*Psittacus erithacus*). *Cognition*, *153*, 146–160.
- Rescorla, R. A., & Cunningham, C. L. (1978). Within-compound flavor associations. *Journal of Experimental Psychology: Animal Behavior Processes*, *4*(3), 267–275.
- Rubin, E. (1921). *Visuell wahrgenommene Figuren*. Copenhagen: Glydenalske Boghandel. (Original work published in Danish, 1915)
- Ruiz, G., & Sánchez, N. (2014). Wolfgang Köhler's The Mentality of Apes and the animal psychology of his time. *The Spanish Journal of Psychology*, *17*, E69.
- Sakiyama, T., & Gunji, Y. P. (2016). The Kanizsa triangle illusion in foraging ants. *Biosystems*, *142*, 9–14.
- Wagemans, J., Elder, J. H., Kubovy, M., Palmer, S. E., Peterson, M. A., Singh, M., & von der Heydt, R. (2012). A century of Gestalt psychology in visual perception I. Perceptual grouping and figure-ground organization. *Psychological Bulletin*, *138*(6), 1172–1217.
- Wasserman, E. A. (1997). The science of animal cognition: Past, present, and future. *Journal of Experimental Psychology: Animal Behavior Processes*, *23*(2), 123.
- Wertheimer, M. (1912). Experimentelle Studien liber das Sehen von Bewegungs. *Zeitschrift für Psychologie und Physiologie der Sinnesorgane*, *61*, 161–265.
- Wertheimer, M. (1923). Untersuchungen zur Lehre von der Gestalt II. *Psychologische Forschung*, *4*, 301–350. Translation published in Ellis, W. (1938). *A source book of Gestalt psychology* (pp. 71–88). London: Routledge & Kegan Paul.

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## Parkinson's Disease

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### Synonyms

[Paralysis agitans](#); [Parkinsonism](#); [PD](#); [Shaking palsy](#)

### Definition

A progressive and degenerative neurological disorder of movement marked by tremors, postural instability, rigidity, and slow movements.

### Introduction

Parkinson's disease is a chronic and relentlessly progressive disease marked by tremors, muscular rigidity, slow movement, and postural instability. Psychiatric problems, such as depression, dementia, and psychosis, may be comorbid to the illness or to a side effect of treatment. Parkinson's is idiopathic and there is no cure, though pharmacological therapy and potentially brain surgery may lessen symptoms (Binder et al. 2009).

## Symptomatology

Parkinson's is recognized for its classic triad of motor symptoms: a resting tremor, rigidity, and bradykinesia (slow movement). The tremors tend to start in the hands, feet, or jaw at 4–6 Hz, start on one side of the body, but eventually progresses to encompass the whole frame. Tremors in the hands are notable for what is called a “pill-rolling tremor”, a rhythmic rubbing and shaking of the forefinger and thumb. Tremors are present at rest and dissipate with intentional movement; sometimes, they can be aggravated by stress. Muscle rigidity in swinging arms presents as short and jerky movements as opposing muscle groups fail to communicate properly and thus remain contracted. This results in stiffness and pain for the patient. Facial rigidity can inhibit the communication of emotions and present as a taut, mask-like face. This triad of bradykinesia, muscle rigidity, and tremors makes daily activities such as dressing and brushing one's teeth very difficult for the patient. In advanced PD, postural instability and issues with balance can lead to frequent falls. Moreover, the progression of Parkinson's leads to the worsening of motor symptoms over time. As patients attempt to keep their balance in later stages, they may present with festination, or the hurrying of steps as they propel themselves forward in walking. Freezing, or the sudden cessation of movement, may also occur in later stages. Though Parkinson's is primarily considered a disorder of movement, other non-



movement symptoms can present themselves and do often complicate the lives of PD patients. Autonomic dysfunction, a decrease in olfaction and taste, mood disorders, sleep disturbances, diminished elements of cognition, and a high risk to dementia in later stages have all been as issues in those with PD (Double and Finberg 2016).

Parkinson's Disease Dementia (PDD) indicates a decline of cognitive functioning that develops over 1 year post-diagnosis, and may be related to Lewy bodies dementia. It is estimated that some 40% of Parkinson's patients struggle with dementia. Risk factors for developing this dementia include advanced age, a later disease onset, a history of smoking, a history of depression, and a poor response to L-Dopa. Deficits in executive functioning and bradyphrenia, or a slowness of thought processes, have both been noted as prominent issues (Kraybill and Suchy 2011).

## Etiology

The etiology, or cause, of Parkinson's disease is very complex and involves multiple factors that may differ widely across patients. Environmental factors have long been suspected, and at one point, viral infection was hypothesized as a cause of idiopathic PD due to a similarity of symptoms involving viral encephalitis. Though the etiology of Parkinson's as related to a number of diverse environmental risk factors remains controversial, a convincing link to a family history of Parkinson's has been demonstrated, suggesting a possible genetic component. Parkinson's disease as a result of one of six genetic mutations has been seen to develop, yet the treatment for genetic Parkinson's is the same as the treatment for common idiopathic Parkinson's. Nevertheless, studies of genetically-transferred Parkinson's patients and their affected family members have provided considerable insight into the neural mechanisms behind the idiopathic form of the disease (Double and Finberg 2016).

## Pathology

Parkinson's neurological presentation is rooted in the dysfunction of the basal ganglia and cerebellum. Subcortical changes, such as the slow loss of dopaminergic neurons in the substantia nigra region of the basal ganglia, are more notable first, followed by cortical changes later in the disease process, which supports the evidence that demonstrates motor symptoms arising earlier than other symptoms. A deposition of Lewy bodies in both subcortical and brainstem areas, such as the substantia nigra, locus ceruleus, nucleus basalis of Meynert, dorsal medial nucleus of the vagus nerve, and hypothalamus, has been recorded in PD patients, though Lewy bodies are certainly not a unique feature in Parkinson's. Alpha-synuclein accumulation in the basal forebrain and ascending pathways, leading to changes in acetylcholine, has been implicated in the cognitive changes in Parkinson's and the onset of Parkinson's dementia (Cook 2017).

## Prevalence

The prevalence of Parkinson's approaches 1% of the total population by age 65, and 2–3% by age 80. Early-onset Parkinson's, diagnosed before age 40, accounts for around 10% of all Parkinson's cases, a statistic that often goes overlooked (Baron 2011). The gender split is roughly 1:1.5, female to male, and as suggested above, age is a major risk factor. Smoking tobacco has been shown to reduce the risk of developing PD (Schwarz and Storch 2009).

## Assessment

A clinical diagnosis of Parkinson's is made after an examination of patient history plus an important physical and neurological battery, conducted by a neurologist, that involves tests for retropulsion and gait monitoring among other diverse measures. Making a differential diagnosis involves weeding out some of the following illnesses, with their distinguishing features in

parentheses: cortical basal degeneration (often with unilateral apraxia and reflex myoclonus), multiple system atrophy (prominent ataxia and autonomic disturbances), progressive supranuclear palsy (issues with vertical eye movement), Wilson's disease (dystonia and liver disease), and Huntington's disease (choreiform movements and family history). A diagnosis of Parkinson's becomes increasingly more probable especially after positive response to levodopa treatment (Cook 2017).

Some presentations of parkinsonism may not be caused by Parkinson's itself, but rather by a psychogenic or pharmacological stimulus. Parkinsonism may stem from a conversion or somatoform disorder or be caused by neuroleptic (dopamine antagonist) therapy used to treat psychotic disorders. However, the Parkinson-like presentation of those who ingest neuroleptics over a long period of time is often bilateral as opposed to the asymmetrical presentation of Parkinson's. Diagnosis of the disease and the gauging of severity are facilitated by one of two standard rating scales: the modified Hoehn and Yahr Scale or the Unified Parkinson's Disease Rating Scale (UPDRS). Post-mortem examination for Parkinson's tends to confirm the diagnosis at a rate of about 80% of those diagnosed with Parkinson's in life (Cook 2017).

## Treatment

Treatments for Parkinson's disease include a wide range of pharmacological therapies, as well as surgery.

### L-Dopa

Levodopa is the amino acid precursor to dopamine that is synthesized by many plants and animals, including humans. Whereas the neurotransmitter dopamine cannot cross the blood-brain barrier, L-Dopa can. It was first implemented in the 1960s and has remained the first-line treatment for PD to this day. L-Dopa works to increase the levels of dopamine in the surviving nigrostriatal neurons of the basal ganglia. It cannot cure PD, yet it can mitigate

motor symptoms in the mild to moderate stages of the disease. The short half-life of L-Dopa necessitates that the patient take regular, evenly-spaced doses throughout the day. Historically, L-Dopa was prescribed orally on its own, with only minimal transference across the blood-brain barrier, thus necessitating very high doses and causing unpleasant side effects like vomiting and nausea. Today, either carbidopa or benserazide, two inhibitors of DOPA decarboxylase, are combined with levodopa to increase its absorption into the brain and reduce these side effects. After some years of symptom reduction with levodopa treatment, the disease progresses and the dosage must be increased to compensate for a continual death of dopaminergic neurons. Elevated levodopa doses are also associated with such side effects as constipation, hypotension, lethargy, hallucinations, and confusion. Dyskinesia, involuntary twisting movements of the arms, legs, and trunk, can result after long-term levodopa therapy. Duodopa pumps that continually pump levodopa into the body have been implanted in recent years to some success (Double and Finberg 2016).

### Glutamate Receptor Antagonists

Glutamate receptor antagonists may be beneficial in the treatment of LID, the dyskinesia associated with levodopa therapy, yet not without a number of pronounced side effects. Nevertheless, with the wide diversity in glutamate subtypes and their distribution across the brain, researchers have not stopped the search for new and selective drug possibilities on this front. The main drug of this class currently in use to treat PD is amantadine, an antiviral with anti-glutamatergic properties (Double and Finberg 2016).

### Dopamine Agonists

In order to alleviate motor symptoms in the later stages of the disease and compensate for the lack of surviving dopaminergic neurons, dopamine agonists are used to directly stimulate the dopamine receptors themselves. Dopamine agonists work by stimulating D2 and also D1 receptors and are primarily taken orally. The side effects associated with dopamine agonists are virtually analogous to those associated with levodopa,

though levodopa is considered more effective at treating symptoms than any dopamine agonist. However, elevated doses of L-Dopa combined with long-term treatment have been associated with increased cell death due to the presence of uncontrolled free radicals. To combat this phenomenon, dopamine agonists and levodopa are sometimes given in tandem in order to reduce the dosage of levodopa and transfer some of that burden onto the stimulation of dopamine receptors by the dopamine agonists (Double and Finberg 2016).

### COMT Inhibitors

Catechol-O-methyl Transferase, or COMT, is a widespread enzyme that serves to break down dopamine, and COMT inhibitors impede this breakdown as a second-line medication for the treatment of Parkinson's (Binder et al. 2009; Double and Finberg 2016). Tolcapone and entacapone are the two drugs available of this type. Entacapone inhibits COMT only peripherally and thus does not cross the blood-brain barrier, unlike tolcapone. The inhibition of COMT in the periphery reduces the metabolism of L-Dopa there, which augments the availability of the drug to the brain. Though tolcapone can cross the barrier and improve the brain's response to L-Dopa by reducing the metabolism to dopamine, there is a significant risk of toxicity to the liver that limits the non-clinical diffusion of this medication. Thus, a common combination of medications for the treatment of Parkinson's is entacapone, L-Dopa, and a previously-mentioned peripheral inhibitor of AADC, like carbidopa (Double and Finberg 2016).

### Deep Brain Stimulation

Deep Brain Stimulation (DBS) involves the implanting of electrodes to stimulate the important areas of the basal ganglia that are most affected by Parkinson's. Detailed electrophysiological studies of the brain's circuitry and interaction between the pallidum, thalamus, and the motor cortex allowed for the development of this technology, as it became apparent that high-rate electrical stimulation could correct the hallmark motor symptoms of the disease. With the proper

equipment, the procedure can be performed in any department of neurosurgery. The implanted electrodes connect to a battery-operated stimulator under the patient's skin, which can be controlled by the patient with a remote, much like a pacemaker for the heart. The procedure is best-suited for those who suffer from an early onset, who are in an advanced stage of the disease, or who do not respond satisfactorily to L-Dopa, and can tolerate the stress of neurosurgery. There are great improvements for many, but the complications can include hardware difficulties and some psychiatric and neurological side effects (Double and Finberg 2016).

### Future Directions in Treatment

Attempts have been made to introduce human embryonic dopamine neurons to be implanted into the Parkinson's brain as a form of treatment. Results in this area have been frustrated by ethical concerns and a lack of satisfactory clinical trials, with side effects that include dyskinesia. Nonetheless, developments in the ideas of stem-cell research continue to be made (Double and Finberg 2016).

Gene therapy, by way of a gene transfer that increases dopamine synthesis or protects the already-existing dopaminergic cells, is a major new frontier in the fight against Parkinson's. This therapy avoids the inherent problem of L-Dopa needing existing presynaptic neurons to encourage dopamine stimulation and involves using a viral vector to introduce new genes into relevant areas of the brain. Early clinical trials are promising and import some benefits to patients. Alternatively, neurotrophic factors such as glial cell line-derived neurotrophic factor (GDNF) can be delivered through genes to bolster dying neurons, yet concerns about safety have led to cautious progress (Double and Finberg 2016).

### Conclusion

Parkinson's disease is a debilitating and pervasive neurodegenerative condition and, while pharmacological and surgical treatment can slow progress, there is no cure. The restoration and

protection of neurons affected is a primary target of investigation, and developing a response to the disease pre-clinically, before symptoms occur, is of particular attention to researchers.

## Cross-References

- ▶ [Dopamine Receptors](#)
- ▶ [Locomotion](#)
- ▶ [Neuron](#)
- ▶ [Neurotransmitters](#)

## References

- Baron, M. S. (2011). Parkinson's disease. In J. S. Kreutzer, J. DeLuca, & B. Caplan (Eds.), *Encyclopedia of clinical neuropsychology* (pp. 1864–1868). New York: Springer.
- Binder, M. D., Hirokawa, N., & Windhorst, U. (Eds.). (2009). Catechol-O-methyl transferase (COMT). In *Encyclopedia of neuroscience* (p. 578). Berlin/Heidelberg: Springer.
- Cook, S. E. (2017). Parkinson's disease. In N. A. Pachana (Ed.), *Encyclopedia of geropsychology* (pp. 1758–1766). Singapore: Springer.
- Double, K., & Finberg, J. (2016). Parkinson's disease. In D. W. Pfaff & N. D. Volkow (Eds.), *Neuroscience in the 21st century* (Vol. XXI, pp. 3843–3861). New York: Springer.
- Kraybill, M., & Suchy, Y. (2011). Parkinson's dementia. In J. Kreutzer, J. DeLuca, & B. Caplan (Eds.), *Encyclopedia of clinical neuropsychology* (pp. 1861–1864). New York: Springer.
- Schwarz, J., & Storch, A. (2009). Parkinson's disease. In F. Lang (Ed.), *Encyclopedia of molecular mechanisms of disease* (pp. 1582–1584). Berlin Heidelberg: Springer.

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# D

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## Declarative Memory

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### Synonyms

[Explicit memory](#)

### Definition

Declarative memory is a long-term memory system where the processes of acquisition, storage, and retrieval are activated voluntarily and consciously.

### Introduction

The study of psychological processes such as learning and perception or memory, among others, has been of interest to many authors throughout history. A considerable amount of theories have been proposed about how these processes work, each of them having more or less empirical support, in many different areas of knowledge. Historically one of the most studied psychological processes that has remained relevant to this day to many researchers is memory. Memory could be defined as a neurocognitive

capability that allows for encoding, storing, and retrieving of information (see Tulving 2000, for more information on the term memory). According to this view, the use of memory implies an initial encoding of information (acquisition), the storage of this information during a determinate time, and its posterior retrieval and use (Anderson 2000).

Although these three components seemingly participate in all memory tasks (Neath and Surprenant 2003), there are two main viewpoints aiming to explain the nature of memory. On one hand, some authors define memory as a unitary process and assume that it adapts its functionality depending on the situation (Masson and MacLeod 1992). In other words, these authors supported the idea that memory is a single system that could operate differently depending on the task at hand, the kind of information, the time available, the subject condition, or the instructions given. On the other hand, it has been argued that memory is composed of different systems and that each one is, or is not, activated in any given situation (Squire 1995). Beyond this theoretical debate (see Foster and Jelicic 1999, for a revision), the study of memory since the middle of the twentieth century supported the idea that, although there are common processes to all memory systems (Neath and Surprenant 2003), it is composed of different and relative independent systems and that each of them have their own characteristics.

## Systems of Memory

One of the first distinctions among the different systems that compose memory was made based on the amount of information stored and the time that this information remains (Hebb 1949). Firstly, short-term memory is defined as the kind of memory that stores information for a brief time lapse. The exact amount of information and the time that it is stored depends on the task at hand, the participant's status, the kind of material used, and many other variables. However, it is accepted that short-term memory could store sets of five to nine elements during a time span of 15–30 s. On the contrary, long-term memory stores a great amount of information, indefinitely. The study of a list of randomly generated numbers, for example, 2-4-5-2-9-7-0-1-1-6-5, and its immediate retrieval could be an example of a short-term memory task. In contrast, long-term memory is used to remember, for example, the name of an old school friend or our telephone number. The distinction between long-term and short-term memory has been supported by studies in many different areas as experimental psychology, neuroscience or studies of patients, to name a few. A third memory system that could be differentiated in accordance with the time that information remains stored is sensory memory. This system keeps the information stored for whatever amount of time needed to be transferred from the perception of the stimuli to its arrival to short-term memory. This process takes just a few hundredths of a second (Walsh and Thompson 1978).

Atkinson and Shiffrin (1968) proposed a well-known memory model in which these three memory systems are integrated. These authors assumed that the information accesses memory through sensory memory, and only some of these pieces of information are transferred to short-term memory. This transfer of information seems to be mediated by an intentional process, and it only selects a small part of the information that is received from the world. Information in short-term memory can be forgotten by decay or replaced by new information. However, rehearsal

can keep it active in this memory system. According to this model, the only information that could generate responses is the one that remains activated in short-term memory. An elaborate rehearsal can allow information to pass from short-term to long-term memory and be stored indefinitely. Finally, information can also be retrieved from long-term to short-term memory and, as it has been mentioned, generate a response. Although the model proposed by Atkinson and Shiffrin (1968) had a deep impact on the study of memory, some data has been found to question some of its assumptions, such as the fact that transference of information through short-term memory is not needed for long-term storage (Shallice and Warrington 1970).

Furthermore, these three systems of memory, namely, sensory, short-term, and long-term memories, have been subdivided into other systems accordingly to some factors such as the type of information stored, the processing of the information, or the way in which the information is acquired, among others. Firstly, there are three systems, specifically sensory memory, iconic, echoic, or haptic, depending on whether the information is visual, auditory, or tactile, respectively. It has been also noted the difference between short-term memory and working memory. It is assumed that while working memory could operate with the stored information, short-term memory only stores and retrieves information without modifying it (Cowan 2008). Adding numbers could be an example of working memory because it requires the individual to keep the information active and operate with it. Finally, a division of long-term memory has been proposed which attends to the kind of processes that carry out the acquisition, storage and retrieval of the information. Moreover, a division of long-term memory has been made depending on whether these processes are activated automatically or if participant's will is required. Following that criterion, long-term memory could be divided into two different systems: non-declarative memory and declarative memory.



## Declarative Versus Non-Declarative Memory

Non-declarative memory, also known as implicit memory or procedural memory, is defined as the system of memory that does not allow the conscious access of information stored; it has a slow acquisition process and is relatively inflexible. Non-declarative memories are acquired and used unconsciously and automatically but, despite this, can have a broad impact in our behavior. Implicit memory could also be divided into other minor systems like the system needed for learning skills and habits or the system for the conditioning of emotional responses. Nonetheless, the most noted implicit memory system is the priming one. In a broader sense, the priming effect consists of the influence of a stimulus previously presented in response to other stimuli without the participant's awareness (see Geva et al. 1997). For example, knowing how to read or ride a bike is a model of non-declarative memories, more specifically procedural memories.

In contrast, declarative memory, also known as explicit memory, is defined as the long-term memory system in which the process of acquisition of information, storage, and retrieval is carried out consciously and voluntarily. These processes are learned rapidly and are more flexible than implicit memory. Declarative memory acquisition and information retrieval are made intentionally, and the information stored could be formulated as propositions or images. Knowing a phone number, a recipe, or the way home or to work is an example of declarative information.

The distinction between declarative and implicit memory has been supported by several studies. For example, different authors argue that amnesic patients who present problems acquiring or storing declarative memories do not present problems to acquire motor (Brooks and Baddeley 1976), perceptible (Cohen and Squire 1980), or cognitive skills (Squire and Frambach 1990). It has also been found that the priming effect appears in amnesic patients (Musen and Squire 1992). In the view of these findings, it could be argued that non-declarative memory is less prone to forgetfulness than declarative memory. Finally,

some authors have proposed that the brain areas that are activated in both systems are different. The most well-known study on this matter is the description that Milner (1966) made about H.M. This patient presented significant deficits in retrieving events that occurred after a brain operation. He could however learn some procedures such as motor skills although he did not remember having learned them. During the operation, H. M.'s hippocampus, hippocampal gyrus, and amygdala were removed. These structures seem to affect the declarative but not the non-declarative memory. This case reveals that the brain areas involved in both systems of memory are different and, also, suggests that those systems are independent. Taking all these studies into account, it can be supported that both systems, declarative and non-declarative, are quite different.

## Two Kinds of Declarative Memory: Semantic and Episodic Memory

More than the memory division exposed above, a distinction has also been proposed between two subsystems of explicit memory depending on the kind of information stored (Tulving 1972). These criteria differentiate between episodic and semantic memory.

Semantic memory stores general information, that is, information that has been learned in the course of our lives and that represents reality and general knowledge. The color of lemons, the order of the numbers, and the name of the capital city of a country are examples of semantic memories. In contrast, episodic memory is a type of declarative memory that stores information such as events, where, how, and when they occur. The most well-known definition of episodic memory was provided by Tulving (2002) who defined this memory system as "a travel back in time." Examples of episodic memory are the memory of a birthday party, a trip made in holidays, or a match played by your favorite team.

A kind of declarative memory is an autobiographical one. It is defined as the storage of information about ourselves, and it is composed of episodic and semantics memories.

Autobiographical memory stores all events that have occurred in our lives and all the information about us. However, although some authors have formulated theories about the principles and functions of autobiographical memory (e.g., Conway 2005), nowadays it is not clear whether autobiographical memory is really different from episodic memory (Markowitsch and Staniloiu 2011), whether it is a subtype of episodic memory (Fivush 2011) or an independent system of memory on its own (Conway and Pleydell-Pearce 2000).

Some authors have criticized the distinction between episodic and semantic memory (McKoon and Ratcliff 1986). However, the distinction of these two systems has been supported through several studies. For example, Spiers et al. (2001) described 147 amnesic patients that presented problems with retrieving episodic memories but not semantic ones. On the contrary, patients have been described to have deficits in semantic but not in episodic memory (for a revision, see Kapur 1999). Despite this, it is usually assumed that, as declarative memory is more sensitive to forgetting than implicit memory, episodic memory is also more easily forgotten than semantic memory. For example, it is more difficult to retrieve the memory of a moment or the context in which the meaning of a word was learned than the meaning of that particular word. Moreover, neuroimaging studies have found that the acquisition of episodic and semantic memories are not activated in the same brain areas, the same way that retrieval episodic or semantic memories are (Wheeler et al. 1997).

However, despite this distinction, it has also been argued that these two kinds of long-term memories are not totally independent from one another and that they could operate jointly. One of the earliest authors proposing this idea was Tulving (1972) who argued that the acquisition of new episodic memories were affected by the information stored in semantic memory. Other authors have proposed a different relationship between semantic and episodic memory. For example, Baddeley (1988) defined semantic memory as the information abstracted and dissociated from various episodic memories (for more

studies that propose interdependence between semantic and episodic memory, see Reder et al. 2009; Mayes and Roberts 2001). In light of these studies, it is clear that these two memory systems operate, to a certain extent, jointly and that memories stored in both declarative memory systems are related in some way.

Finally, keeping in mind that the division of the different memory systems is not supported by all authors, declarative memory could be defined as the kind of long-term memory that is acquired, stored, and retrieved consciously and voluntarily. Declarative memory could be divided into three subsystems: semantic, episodic, and autobiographic memory, each of them storing general knowledge, information about events or the information about ourselves.

## Cross-References

- ▶ [Long-Term Memory](#)
- ▶ [Memory](#)
- ▶ [Priming](#)
- ▶ [Retrieval](#)
- ▶ [Short-Term Memory](#)
- ▶ [Working Memory](#)

## References

- Anderson, J. R. (2000). *Learning and memory*. New York: Wiley.
- Atkinson, R. C., & Shiffrin, R. M. (1968). Human memory: A proposal system and its control processes. In K. W. Spence & J. T. Spence (Eds.), *The psychology of learning and motivation* (Vol. 8). London: Academic.
- Baddeley, A. D. (1988). Cognitive psychology and human memory. *Trends in Neurosciences*, *11*, 176–181.
- Brooks, D. N., & Baddeley, A. D. (1976). What can amnesic patients learn? *Neuropsychologica*, *14*, 111–122.
- Cohen, N. J., & Squire, L. R. (1980). Preserved learning and retention of pattern-analyzing skill in amnesia: Dissociation of “knowing how” and “knowing that”. *Science*, *210*, 207–209.
- Conway, M. (2005). Memory and the self. *Journal of Memory and Language*, *53*(4), 594–628.
- Conway, M., & Pleydell-Pearce, C. (2000). The construction of autobiographical memories in the self-memory system. *Psychological Review*, *107*(2), 261–288.

- Cowan, N. (2008). What are the differences between long-term, short-term, and working memory? *Progress in Brain Research*, 169, 323–338.
- Fivush, R. (2011). The development of autobiographical memory. *Annual Review of Psychology*, 62, 559–582.
- Foster, J. K., & Jelicic, M. (1999). *Memory: Systems, process, or function? Debates in psychology*. New York: Oxford University Press.
- Geva, A., Moscovitch, M., & Leach, L. (1997). Perceptual priming of proper names in young and older normal adults and a patient with prosopagnosia. *Neuropsychology*, 11(2), 232–242.
- Hebb, D. O. (1949). *The organization of behavior*. New York: Wiley.
- Kapur, N. (1999). Syndromes of retrograde amnesia: A conceptual and empirical synthesis. *Psychological Bulletin*, 125, 800–825.
- Markowitsch, H., & Staniloiu, A. (2011). Memory, auto-noetic consciousness, and the self. *Consciousness and Cognition*, 20(1), 16–39.
- Masson, M. E. J., & MacLeod, C. M. (1992). Reenacting the route to interpretation: Enhanced perceptual identification without prior perception. *Journal of Experimental Psychology: General*, 121, 145–176.
- Mayes, A. R., & Roberts, N. (2001). Theories of episodic memory. *Philosophical Transactions of the Royal Society of London B*, 356, 1395–1408.
- McKoon, G., & Ratcliff, R. (1986). Automatic activation of episodic information in a semantic memory task. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 12, 108–115.
- Milner, B. (1966). Amnesia following operation on the temporal lobes. In C. W. M. Whitty & O. L. Zangwill (Eds.), *Amnesia* (pp. 109–133). London: Butterworth.
- Musen, G., & Squire, L. R. (1992). Nonverbal priming in amnesia. *Memory, and Cognition*, 20(4), 441–8.
- Neath, I., & Surprenant, A. (2003). *Human memory: An introduction to research, data and theory*. Belmont: Wadsworth.
- Reder, L. M., Park, H., & Kieffaber, P. D. (2009). Memory systems do not divide on consciousness: Reinterpreting memory in terms of activation and binding. *Psychological Bulletin*, 135, 23–49.
- Shallice, T., & Warrington, E. K. (1970). Independent functioning of verbal memory stores: A neuropsychological study. *Quarterly Journal of Experimental Psychology*, 22, 261–273.
- Spiers, H. J., Maguire, E. A., & Burgess, N. (2001). Hippocampal amnesia. *Neurocase*, 7, 357–382.
- Squire, L. R. (1995). Biological foundations of accuracy and inaccuracy of memory. In D. L. Schacter (Ed.), *Memory distortions* (pp. 197–225). Cambridge, MA: Harvard University Press.
- Squire, L. R., & Frambach, M. (1990). Cognitive skill learning in amnesia. *Psychobiology*, 18, 109–117.
- Tulving, E. (1972). Episodic and semantic memory. In E. Tulving & W. Donaldson (Eds.), *Organization of memory* (pp. 382–402). New York: Academic.
- Tulving, E. (2000). Concepts of memory. In E. Tulving & F. I. M. Craik (Eds.), *The Oxford handbook of memory* (pp. 33–43). New York: Oxford University Press, Inc..
- Tulving, E. (2002). Episodic memory: From mind to brain. *Annual Review of Psychology*, 53, 1–25.
- Walsh, D., & Thompson, L. (1978). Age differences in visual sensory memory. *Journal of Gerontology*, 33 (3), 383–387.
- Wheeler, M. A., Stuss, D. T., & Tulving, E. (1997). Toward a theory of episodic memory: The frontal lobes and auto-noetic consciousness. *Psychological Bulletin*, 121, 331–354.

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# H

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## Habituation

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### Synonyms

[Desensitization](#); [Nonassociative learning](#)

### Definition

Habituation refers to a decrease in behavioral responding as a result of repeated exposure to a stimulus that is not attributed to sensory adaptation or motor neuron fatigue.

### Introduction

Have you ever been stuck on a noisy train car? When you first got on the train, you were probably annoyed by the conductor's loud voice over the speaker, the screeching sounds of the train as it stops and starts, or the person next to you yelling into her phone. However, as the ride went along, you probably stopped paying attention to the loud noises and may have forgotten about how annoying these noises were when you first boarded the train. This is an example of habituation. Habituation is the basic learning mechanism involving a decrease in responding with repeated

presentations of a stimulus (Domjan 2015). Habituation typically helps an organism ignore stimuli within their environment after learning a stimulus is not biologically relevant. From the example above, you might learn to ignore the train sounds or the person on the phone because they do not have a direct impact on you. You might even forget what the conductor said over the loud speaker or what the person was yelling about on the phone.

### Characteristics

A number of characteristics have been identified to explain how various factors impact the process and strength of the habituation process. Habituation can occur for varying amounts of time. Short-term habituation generally occurs when a response-eliciting stimulus is presented repeatedly within short intervals, while long-term habituation occurs with delayed but continuous presentations of a stimulus. Long-term habituation persists for longer periods of time and is generally attributed to enduring changes in learning compared to short-term habituation, which can dishabituate\* relatively quickly (Domjan 2015). Long-term and short-term habituation rely on different neural mechanisms, which can be attributed to the differences in the strength of habituation for each process (Squire 1987). Habituation can also be affected by time through spontaneous recovery\* (this is the identifying

characteristic of short-term habituation). If an organism is habituated to a stimulus and shows a decrease in responding, the response can at least partially recover with the passage of time (Thompson and Spencer 1966). Habituation can occur more quickly after the presentation of multiple stimulus-response presentations followed by spontaneous recoveries. Spontaneous recovery occurs faster for habituation resulting from high stimulation frequencies than habituation resulting from the presentation of low frequencies of stimulation (Rankin et al. 2009). The stronger the stimulus, the less likely habituation will occur, while weaker stimuli allow habituation to occur more quickly, showing a stronger decrease in the response. Habituation training that continues to occur after the response to a stimulus has disappeared or remained constant will result in slower recovery of the behavioral response (Thompson and Spencer 1966). Habituation for one response to a stimulus can also generalize toward other, similar stimuli. When presented with a separate (and usually stronger) stimulus, the stimulus will elicit the recovery of habituation (or decreased responding) to the original stimulus, also known as the process of dishabituation (Rankin et al. 2009). When the dishabituating stimulus is repeatedly presented to the organism, this can lead to a reduction in dishabituation, allowing the organism to habituate to the stimulus once again.

Habituation is not the only type of learning involving decreased responses to a stimulus.

A decrease in responding to a stimulus is considered habituation if it cannot be attributed to sensory adaptation or motor neuron fatigue. Sensory adaptation\* occurs when the sensory organs temporarily fail to respond to a stimulus. Sensory adaptation can occur when you enter a dark room and have trouble seeing because your eyes have not adjusted to the change in light. Motor neuron fatigue occurs when the muscles are temporarily unable to make the response to a given stimulus. Motor fatigue can occur if you are touching a vibrating object and you stop feeling the vibration because your motor neurons have weakened. Both of these concepts are not considered habituation, in part because they occur outside of the nervous

system. During habituation, the organism no longer responds but is still fully capable of sensing the stimulus and making the muscle movements required for the response (Domjan 2015).

Habituation can also be distinguished from motor neuron fatigue because habituation is *stimulus* specific. To rule out motor neuron fatigue, we look at different stimuli. If the organism does not produce a response to a stimulus, but can produce the same response to a different stimulus, the decline of the target response cannot be explained as response fatigue (Domjan 2015). A study by Epstein et al. (1992) illustrates this point. During this study, female participants were exposed to a repeated stimulus (tasting lemon or lime juice) for 10 trials. As the trials progressed, responding (amount of salivation) decreased over the course of 10 trials. At test, participants were exposed to a novel stimulus (the flavor they did not receive during the initial trials). After exposure to a novel stimulus, participants showed a significant recovery in responding (i.e., salivation). Results from this study showed that participants habituated to the repeated stimulus (i.e., the familiar flavor), and the salivation response could be restored with the presentation of a novel flavor.

Habituation can be distinguished from sensory adaptation because habituation is *response* specific. To rule out sensory adaptation, we look at different responses elicited by the same stimulus: If the organism does not produce a certain response to a stimulus, but still produces other responses to the same stimulus, the decline of the target response cannot be explained as sensory adaptation (Domjan 2015). For example, in the study by Epstein et al. (1992), repeated exposure to a flavor (either lemon or lime juice) resulted in a decrease in not only salivation but also a second response, namely, hedonic ratings. Had the authors observed a decline in only one of these responses (e.g., decrease in salivation, but not in hedonic ratings), their experiments would have also ruled out sensory adaptation.

Neuroscience research shows evidence supporting the role of neural mechanisms in the habituation process (see Kandel 2000; Thompson and Spencer 1966). While sensory adaptation occurs in the sensory organs and motor neuron

fatigue occurs in the effector muscles, habituation occurs within the nervous system\*. An organism fails to respond when habituation occurs due to changes in the nervous system, which prevent sensory neural impulses from reaching the motor neurons to perform a response (Domjan 2015). For example, Kupfermann and Kandel (1969) examined how behavior is modified by neuron activity by observing behavior in *Aplysia*, a species of sea snail. Their focus was on the process of sensitization\* – a fear response that emerges when an animal learns to produce strong responses to a neutral stimulus. Specifically, they examined the defense reflex, which involves gill withdrawal in response to aversive stimuli. *Aplysia* will withdraw their gills when they encounter a tactile stimulus to a specific part of the body known as the siphon. When an aversive shock was applied to the tail, *Aplysia* identified this as dangerous and evoked the defense reflex. However, when a neutral stimulus was applied to the *Aplysia*, the animal still produced a strong response to the stimulus. Results from this study suggest that *Aplysia* did not habituate to the stimuli but evoked strong defense reactions toward aversive (and nonaversive) stimuli. Kandel (2000) also showed that the process of long-term and short-term memory for sensitization differs. Long-term memory requires new proteins to be synthesized and is determined by the number of repeated exposures to the aversive stimulus. Repeated exposure to aversive stimuli with the implementation of a short delay between each presentation led to longer duration of memory for the aversive stimulus, lasting for days. In contrast, a single exposure to an aversive stimulus generated short-term memory of the stimulus, lasting only a few minutes. While research finds evidence linking habituation, learning, and neuroscience, more research is needed to fully understand *how* these mechanisms contribute to the learning process.

## Theoretical Support

The dominant theory for the underlying causes of habituation is known as the *dual-process theory*. Proposed by Groves and Thompson (1970), the

dual-process theory states that both increases and decreases in responding to a stimulus are guided by specific neurological processes. The theory suggests that habituation is guided by a process that decreases responding to a stimulus, while sensitization leads to increases in responding to a stimulus. Groves and Thompson suggested that each process occurs in distinct parts of the nervous system. While sensitization occurs in the state system, to determine the readiness of an organism to respond to a stimulus, habituation occurs in the S-R system, which allows an organism to make a specific response to a stimulus. The S-R system is activated for each stimulus eliciting a response while the state system is only activated in the presence of arousing stimuli. According to this theory, habituation and sensitization each attempt to control behavior, and the specific behavior elicited is determined by the net result of both processes (Domjan 2015). If a decrease in behavior emerges, this suggests that the strength of the habituation process is stronger than the strength of the sensitization process, leading to decreases in responding.

## Cross-References

- ▶ [Dishabituation](#)
- ▶ [Nervous System](#)
- ▶ [Sensitization](#)
- ▶ [Sensory Adaptation](#)
- ▶ [Spontaneous Recovery](#)

## References

- Domjan, M. (2015). *The principles of learning and behavior*. Stamford: Cengage Learning.
- Epstein, L. H., Rodefer, J. S., Wisniewski, L., & Caggiula, A. R. (1992). Habituation and dishabituation of human salivary response. *Physiology & Behavior*, 51(5), 945–950.
- Groves, P. M., & Thompson, R. F. (1970). Habituation: A dual-process theory. *Psychological Review*, 77(5), 419–450.
- Kandel, E. R. (2000, December). The molecular biology of memory storage: A dialog between genes and synapses, *Nobel Lecture*. Lecture conducted from Howard



- Hughes Medical Institute, Columbia University, College of Physicians and Surgeons, New York.
- Kupfermann, I., & Kandel, E. R. (1969). Neuronal controls of a behavioral response mediated by the abdominal ganglion of *Aplysia*. *Science*, *164*(3881), 847–850.
- Rankin, C. H., Abrams, T., Barry, R. J., Bhatnagar, S., Clayton, D., Colombo, J., Coppola, G., Geyer, M. A., Glanzman, D. L., Marsland, S., McSweeney, F., Wilson, D. A., Wu, C., & Thompson, R. F. (2009). Habituation revisited: An updated and revised description of the behavioral characteristics of habituation. *Neurobiology of Learning and Memory*, *92*(2), 135–138. doi:10.1016/j.nlm.2008.09.012.
- Squire, L. R. (1987). *Memory and brain*. New York: Oxford University Press.
- Thompson, R. F., & Spencer, W. A. (1966). Habituation: A model phenomenon for the study of neuronal substrates of behavior. *Psychological Review*, *73*(1), 16.

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# E

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## Event-Related Potentials (ERPs)

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### Definition

Event-related potentials, or ERPs, are the resulting of average the *EEG* signal (see “► [EEG](#),” this volume) locked to a specific event. Therefore, the main function of ERPs is to *study* the brain activity that is elicited because of that event, while it is discarded, the brain activity elicited for everything else. The event under analysis typically is the perception of a stimulus (e.g., an image or sound) (e.g., Thorpe et al. 1996), or the emission of an overt response (e.g., Gehring et al. 1993), although the EEG signal can be locked to covert (internal) responses as, for instance, inner speech (Ford and Mathalon 2004).

### Advantages and Disadvantages of the ERPs Technique

Because ERPs are generated from the EEG signal, the use of ERPs has the same advantages and disadvantages described for the EEG test (see “► [EEG](#),” this volume). In brief, EEG is good for studying cortical brain activity with great temporal resolution and is noninvasive and inexpensive. On the other hand, the most important

disadvantages of using EEG are its poor spatial resolution and that it is not appropriate for studying subcortical brain areas.

We might add another drawback for the ERPs technique. ERPs work under the assumption that the EEG signal locked to an event contains both a “true” signal from the brain and some degree of noise. The noise is not elicited because of the event and therefore should take different values each time that the event takes place. Therefore, given a sufficient number of repetitions of the event or *trials*, the average data from all these trials should reflect only *event-related* true signal, since recordings of noise should cancel each other. The number of event repetitions that you need in order to wipe out all the noise depends on the signal/noise ratio. In most of the cases, the number of event repetitions needed for proper ERPs analysis is relatively high, although it depends on the *components* under study (see below). Consequently, ERPs experiments are usually very long and need many trials. This makes the ERPs technique hard to use for the study of some topics. That is the case, for example, if you are interested in the brain activity associated with the first learning episode of some specific content (you can only learn something for the first time once, although see Luque et al. 2012).

An important advantage of using ERPs is that you can use it for studying *covert* events. That is, you do not need overt responses to register your dependent variable. This feature, plus the great temporal resolution of EEG, makes ERPs a great

tool for studying the first stages of perceptual/attentional processing (Luck et al. 2000).

## Components

ERPs signal, after the averaging process described before, takes the form of a sequence of positive and negative deflections in voltage. Importantly, this sequence is usually the same for events of the same type (visual events, overt responses, etc.). These deflections are usually called peaks, waves, or *components*. ERPs components were named depending on whether the peak is positive or negative and reflecting the approximate latency of the peak (from the onset of the event). For instance, the N200 component stands for a negative wave (hence the *N*) with its maximal amplitude (peak) at 200 ms after the onset of the event. The latency of each component is only approximate, what makes components' names sometimes confusing (it is not rare to find a P300 component peaking at 500 ms). To make things more complicated, sometimes the ordinal position of the component in the sequence of peaks is used to name the component, instead of the latency in milliseconds (e.g., P3 would be the third positive peak).

Numerous ERPs studies have investigated the psychological meaning of these components, with variable success. In general, there is agreement that early components (peaking sooner than 200 ms) are easier to relate with underlying psychological processes. For instance, the P1 and N1 components reflect rapid deployment of attention and the first stages of perceptual processing (Hillyard and Anllo-Vento 1998).

The more important ERPs components in cognitive neuroscience are (among others) the

aforementioned P1 and N1, the N2 and the mismatch negativity (which might reflect the detection of a perceptual deviant), the P3 (which has been related with working memory), and the N400 (elicited by semantically incongruent stimuli) (for more information, see Luck and Kappenman 2011).

## Cross-References

► EEG

## References

- Ford, J. M., & Mathalon, D. H. (2004). Electrophysiological evidence of corollary discharge dysfunction in schizophrenia during talking and thinking. *Journal of Psychiatric Research*, 38(1), 37–46.
- Gehring, W. J., Goss, B., Coles, M. G., Meyer, D. E., & Donchin, E. (1993). A neural system for error detection and compensation. *Psychological Science*, 4(6), 385–390.
- Hillyard, S. A., & Anllo-Vento, L. (1998). Event-related brain potentials in the study of visual selective attention. *Proceedings of the National Academy of Sciences*, 95(3), 781–787.
- Luck, S. J., & Kappenman, E. S. (Eds.). (2011). *The Oxford handbook of event-related potential components*. New York: Oxford University Press.
- Luck, S. J., Woodman, G. F., & Vogel, E. K. (2000). Event-related potential studies of attention. *Trends in Cognitive Sciences*, 4(11), 432–440.
- Luque, D., López, F. J., Marco-Pallares, J., Càmarà, E., & Rodríguez-Fornells, A. (2012). Feedback-related brain potential activity complies with basic assumptions of associative learning theory. *Journal of Cognitive Neuroscience*, 24(4), 794–808.
- Thorpe, S., Fize, D., & Marlot, C. (1996). Speed of processing in the human visual system. *Nature*, 381(6582), 520–522.

# E

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## EEG

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### Synonyms

[Electroencephalogram](#); [Electroencephalography](#)

### Definition

EEG stands for both electroencephalogram and for electroencephalography. While electroencephalography is the name of a *test* (see below), electroencephalogram is the resulting signal from that test. Electroencephalography measures the electric field that is naturally elicited by brain activity, usually recorded at scalp level. However, in animal research and in some medical applications, invasive intracranial recording is sometimes used.

### What is Registered by the EEG Test?

Neurons communicate each other through so-called nerve impulses or *action potentials* (see “► [Action Potentials](#),” this volume). EEG signal is rarely produced by these action potentials themselves. On the contrary, EEG electrodes register the electrical activity produced by the chain of biochemical processes originated as a

consequence of the *action potentials*. Without getting in too much detail, action potentials produced neurotransmitters that bind to receptors, what changes the extra- and intracellular ionic flow of neurons, in what is known as *postsynaptic potentials*. During *postsynaptic potentials*, the ionic concentration outside neurons becomes unevenly distributed, what makes them a dipole with positive and negative charged ends (or poles) (for more detail see Buzsáki et al. 2012). Dipoles generate an electromagnetic field. EEG electrodes can detect this electric signal, while *magnetoencephalography* devices are able to detect the magnetic field.

The electric signal elicited by one neuron is too weak to be detected by EEG, especially when the EEG signal is noninvasively measured at scalp level. Only when a large number (millions) of neurons are active at the same time, the sum of all these small electric fields forms a dipole strong enough for being detected by the EEG electrodes placed at the scalp. Importantly, electric fields only add each other when they have the same orientation (otherwise, they cancel each other). For this reason, EEG signal is produced by brain structures in which neurons share the same spatial alignment. Brain areas with such regular structures are mostly in the cerebral cortex. For this reason, the EEG test is useful for the study of cortical brain activity, and it is considered not suitable for the study of subcortical regions (see Luck 2005). Thus, in brief, we could say that the EEG test measures the electric field produced by

the sum of millions of postsynaptic potentials in the cerebral cortex.

### Advantages and Disadvantages of the EEG Test

One of the greatest advantages of using EEG is its great temporal resolution, in the range of the millisecond (or even better for intracranial measurements). Therefore, the use of EEG is especially appropriate if you are interested in knowing *when* certain brain activity occurs (see “► [Event Related Potentials \(ERPs\)](#),” this volume). However, EEG spatial resolution is low as compared with other neuroimaging techniques (e.g., fMRI). The reason for this is that, given a specific EEG distribution at scalp level (i.e., a 2D map of differences in voltage), there are an infinite number of possible combinations of dipoles (in a 3D space) that could cause it. This has been known as the *inverse problem in EEG*, and, although several mathematical tools have been proposed to solve it (see Grech et al. 2008), it is still advisable to combine EEG with other neuroimaging techniques (e.g., fMRI) if you are interested in the neural generators of the EEG signal. The other important limitation of EEG is that it cannot register neural activity from subcortical brain areas.

However, the EEG test has advantages that make it very popular in both research and medical contexts. The EEG test is relatively inexpensive and is noninvasive, and it can be easily combined with other techniques, such as eye-tracking or fMRI.

### Most Common Uses

EEG is used for both research and medical purposes. In research, EEG is widely used in the form of *event-related potentials* (see “► [Event Related Potentials \(ERPs\)](#)”). In addition, sleep research has been greatly benefited of the use of EEG. For instance, EEG is used to discriminate and study sleep stages. In medical context, EEG is used in several clinical circumstances, for instance, for epilepsy diagnosis and monitoring and for monitoring brain activity of patients in a coma or a vegetative state.

### Cross-References

- [Action Potentials](#)
- [Event Related Potentials \(ERPs\)](#)
- [Evoked Potentials](#)

### References

- Buzsáki, G., Anastassiou, C. A., & Koch, C. (2012). The origin of extracellular fields and currents – EEG, ECoG, LFP and spikes. *Nature Reviews Neuroscience*, 13(6), 407–420.
- Grech, R., Cassar, T., Muscat, J., Camilleri, K. P., Fabri, S. G., Zervakis, M., . . . , & Vanrumste, B. (2008). Review on solving the inverse problem in EEG source analysis. *Journal of Neuroengineering and Rehabilitation*, 5(1), 25.
- Luck, S. J. (2005). *An introduction to the event-related potential technique*. Cambridge, MA: The MIT Press.

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# M

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## Myelination

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A thick insulating structure derived by the glial cells around the axons of neuron cells in the nervous system is called myelin. The overall event of myelin formation is called myelination.

Myelin was first described by Rudolf Virchow in 1864. It is made up of 70% of lipid (neutral lipids, phosphoglycerides, sphingolipids) and 30% of proteins (majorly glycoproteins). Myelin sheath is derived from the plasma membrane of the glial cells. In the central nervous system (CNS), it is formed by oligodendrocytes, while in the peripheral nervous system (PNS), it is formed by Schwann cells. It is not that all the axons of vertebrate is myelinated, even the non-myelinated axons have their role in nervous system. The fundamental role of myelin sheath is to fast conduction of action potential along the neurons which it insulates (Fields 2014). There will be a periodic gap in the myelin sheath between adjacent myelin segments – node of Ranvier. These gaps or nodes are rich in sodium and chloride ion channels. Action potential is triggered at these nodes and passively move to the next node where the next action potential is generated; this jumping of action potential from node to node

results in rapid conduction of nerve impulses (Kettenmann and Verkhratsky 2011).

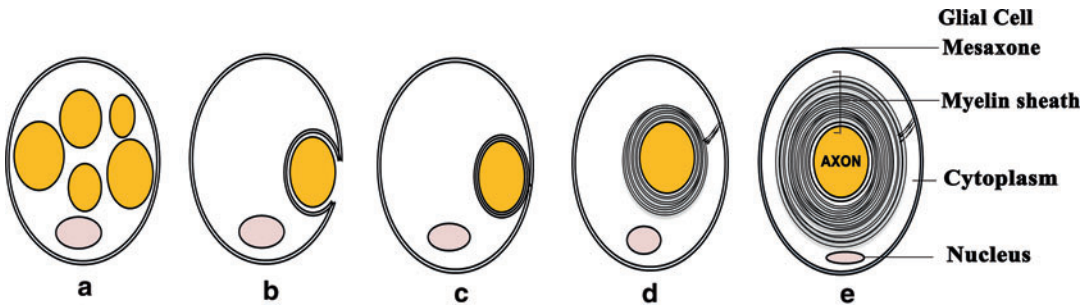
## Early Events in Myelination

Myelination is a complex molecular process that requires precious coordination between several cellular signaling molecules and cascades. Glia-axon interactions are potentially vital throughout the event of myelination. Signaling molecules like neuregulins, neurotrophic factors, transcription factors, and survival factors are required in myelinating of axons (Feltri et al. 2016). Early events in myelination involve different morphological stages, where every stage is highly controlled and well executed by the specific signaling molecules both in the central and peripheral nervous system (Fig. 1).

## Myelination in CNS

In the CNS, myelination process is carried by the oligodendrocytes and their precursor, where single oligodendrocyte can myelinate multiple axons; therefore, it is called as multipolar glia. Myelin sheath is formed by the plasma membrane of oligodendrocytes that spirally wrap around the axon that have a diameter of more than 0.2  $\mu\text{m}$ , to form thick insulating structure of around 40 segments (Simons and Trajkovic 2006). Oligodendrocytes are developed from oligodendrocyte





**Myelination, Fig. 1** Early events of myelination in the CNS and PNS. (a) Bundles of axons are closely associated with glial cells. (b) Glial cells surround the single axon. But the mesaxon is not yet completely fused but portion of

axon is engulfed. (c, d) The mesaxon is fused in the initial stage; later the glial cells begin to rotate around the axon to form few layer of myelin. (e) Myelin completely wraps around the axon to form tightly packed myelin sheath

progenitor cells (OPCs) that divide and migrate to the appropriate destination from their germinal region, and then initiation of myelin component's synthesis will take place. Later myelin wrapping will be initiated, followed by compaction of myelin structure by mature oligodendrocytes. Many extrinsic and intrinsic signals control the oligodendrocyte differentiation and myelination (Emery 2010). Signaling molecules like neuregulins-1 (NRG1), laminin, PDGF, IGF, NT, and Notch-1 (Barres and Raff 1999) are expressed during the myelination in the CNS. Recent studies on the role of oligodendrocytes have proven that initiation and continued myelination can be done by oligodendrocytes in the absence of neurons. This proves the major function of oligodendrocytes in myelinating the axons of CNS.

## Myelination in PNS

Schwann cells are the glial cells of the PNS; their plasma membrane differentiation forms the myelin sheath around the axons of peripheral neurons. In PNS, a single Schwann cell will myelinate a single axon. Neuronal crest cells are the stem cells which generate the Schwann cell precursors that migrate along the axons extending to their target. In the next step, this Schwann cell precursor gives rise to immature Schwann cell which performs the radical sorting of axons. This allows the axons to build one-to-one relationship stable contact between the axons and Schwann cells. Later

Schwann cells which are in promyelinating stage will form the tight wrapping of myelin around the axon to form myelinated Schwann cell. The signaling molecules like nucleic acid-binding (NAB) protein, Sox-10, Krox-20, Oct-6, Brn1, and Brn2 are involved in the myelination of peripheral neurons (Jessen and Mirsky 2005).

## Conclusion

Myelination is a step-by-step event that is highly coordinated by several intrinsic and extrinsic factors. Many neuropathic diseases exhibit the demyelinated morphological characteristic that fails in normal conduction of nerve impulse. Thus myelin development and their maintenance are considered very crucial in healthy individuals. Still the cellular and molecular mechanisms involved in myelination and their maintenance are likely to be key area for further research.

## Cross-References

- ▶ [Axons](#)
- ▶ [Myelin sheath](#)
- ▶ [Oligodendrocytes](#)
- ▶ [Schwann cells](#)

## References

- Barres, B. A., & Raff, M. C. (1999). Axonal control of oligodendrocyte development. *The Journal of Cell Biology*, 147(6), 1123–1128.
- Emery, B. (2010). Regulation of oligodendrocyte differentiation and myelination science. *Science*, 330(6005), 779–782.
- Feltri, M. L., Poitelon, Y., & Previtali, S. C. (2016). How Schwann cells sort axons: New concepts. *The Neuroscientist*, 22(3), 252–265.
- Fields, R. D. (2014). Myelin formation and remodeling. *Cell*, 156(1–2), 15–17.
- Jessen, K. R., & Mirsky, R. (2005). The origin and development of glial cells in peripheral nerves. *Nature Reviews Neuroscience*, 6(9), 671–682.
- Kettenmann, H., & Verkhratsky, A. (2011). Neuroglia – Living nerve glue. *Fortschritte der Neurologie Psychiatrie*, 79(10), 588–597.
- Simons, M., & Trajkovic, K. (2006). Neuron-glia communication in the control of oligodendrocyte function and myelin biogenesis. *Journal of Cell Science*, 119(21), 4381–4389.

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# O

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## Occlusion

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### General Information

Occlusion derives from the Latin *occludere*, a verb that means “to close up.” Its origin should provide an obvious hint regarding its utilization in the modern day: when something is occluded, it is blocked off or obstructed (McCoy 2013). Vascular occlusion, which occurs when a blood vessel is clogged, is responsible for many morbidities commonly associated with ischemia. Ischemia occurs when blood supply to tissues is restricted, depleting the downstream tissue of molecules like oxygen and glucose needed to keep the tissue alive through cellular metabolism. A common example of an occlusion is that of a coronary artery, called a myocardial infarction, that leads to heart attacks; the occluding agent in heart attacks is often a blood clot that blocks the passage through the artery, obstructing blood flow (Ferdinandy et al. 2014).

Common jargon related to occlusion includes terms like thrombus, embolus, ischemia, and infarction. A thrombus is a blood clot that forms in the blood stream or in the heart, while an embolus can be anything that travels in the blood vessel until it reaches a vessel too narrow to let the object pass. When the object cannot pass through

this smaller vessel, an embolus blocks blood flow and leads to occlusion. An embolus can be a myriad of objects such as fat, a tumor, or even a foreign object. When a piece of a blood clot breaks off and then gets stuck due to a narrow vessel, this agent is referred to as a thromboembolus because it is a blood clot that formed in the artery or vein and was too large to continue through the blood vessels. As expected, an embolus is more common in narrower arteries (Welch 1899). Recall that ischemia is the result of a decrease of blood supply to tissue that results in tissue dysfunction or even death due to the depletion of metabolic nutrients. An infarction results from prolonged ischemia and refers to the death of tissue due to the loss in blood supply (Fluri et al. 2015).

### Occlusion and Stroke

Stroke incidence and related fatality rates have been in a decline due to several implemented measures meant to control cardiovascular risk factors such as cholesterol or smoking cessation programs (Mozaffarian et al. 2016). In addition, the decline can be contributed to improved prevention and care once acute strokes occur (Jauch et al. 2013). While the decline in the number of stroke in the USA has fallen around 18.2% and the fatality rate has declined by 33.7%, this does not mean strokes are not as impactful on the population. This substantial decline has only lead to

stroke becoming the fifth leading cause of ► **death** in the USA, instead of fourth. In fact, it has been reported that in 2013, 1 in 20 deaths in the USA were due to stroke, with a stroke occurring every 40 seconds and a death due to stroke occurring every 4 minutes in the USA alone (Mozaffarian et al. 2016). Still, this is a major improvement from just 5 years prior, as stroke was ranked as the third leading cause of death in the USA in 2008 (Jauch et al. 2013).

Like myocardial infarctions, large strokes are usually the result of at least one large vessel occlusion that leads to decreased blood flow and eventually ischemic injury regions of the brain such as the ► **hippocampus** or the ► **hypothalamus**. These ischemic strokes are referred to as cerebral infarctions. Brain imaging is often a priority to understand the location and size of the occlusion. Occlusion of a large vessel, such as the middle cerebral artery or MCA, leads to increased density in a CT scan of the brain. A large vessel occlusion often causes a severe stroke and helps predict neurological deterioration. A hyper-dense MCA can be seen in up to half of thromboses, or blood clotting (Jauch et al. 2013).

### **Animal Models of Ischemic Stroke Involving Occlusion**

Due to the significant effect of strokes on society, there is a keen interest in the scientific community to study the effects of large vessel occlusion in arteries such as the MCA. Due to the nature of occlusion studies, it is easier to study the mechanisms of occlusion and stroke in animals than it is to experiment with the effects of large vessel occlusions on human participants due to concern for ► **welfare**. Studies using animal models have greatly expanding the knowledge around mechanisms of occlusion and have proven to be of great benefit to stroke patients. Rats and mice commonly serve as models of ischemic strokes, but there exist many different animal models. The use of animal models in stroke research has aided our understanding of the physiology and pathology of stroke in humans. Many of these animal models are considered induced models, a term that refers

to animals in which the condition is caused experimentally. For the rats used in many occlusion studies, an occlusion is introduced that induces the stroke (Casals et al. 2011).

There are many occlusion mechanisms to induce ischemia, such as blood vessel constriction, infarction, middle cerebral artery (MCA) occlusion, and macrosphere embolization. MCA occlusion is performed by injecting blood clots to obstruct circulation through a carotid artery into the head, which then go on to block blood flow. Artificial macrospheres between 100 and 400  $\mu\text{m}$  model occlusion of the MCA using sutures, while microspheres around 20 to 50  $\mu\text{m}$  occlude smaller vessels. Macrospheres are injected into the internal carotid artery and lead to focal, or localized, ischemic lesions, while microspheres are inserted into either the MCA or the internal carotid artery and lead to multifocal infarcts. These artificial spheres are injected into vessels to obstruct blood flow and induce ischemia, like the injection of blood clots (Fluri et al. 2015).

Endovascular filament middle cerebral artery occlusion is an animal model specific to rats and later adapted for mice of focal cerebral ischemia that was developed in 1986. It consists of a filament or intraluminal suture that obstructs blood flow when inserted into the vessel at the base, or origin, of the MCA; the occluding agent can be inserted and removed periodically at will to restore or obstruct blood flow, or left in the vessel permanently. When the MCA is reperfused, or re-oxygenated, via the withdrawal of the suture, this is referred to as transient middle cerebral artery occlusion. The longer the artery is occluded, the more severe the ischemic change in the tissues that the artery leads to (Ansari 2011).

### **Other Forms of Occlusion**

Occlusion is not specific to the blockage of blood vessels and is used in dentistry and visual psychology as well. ► **Dental** occlusion refers to how the upper and lower teeth touch each other when the jaw is closed, with malocclusion referring to when the teeth do not close properly (McCoy 2013). The occlusion of a retinal artery

slows blood flow to the retina, causing vision loss in the ischemic retina due to dysfunctional tissue (Moshiri 2015). External of our body, visual occlusion occurs when a view is obstructed in some shape of form. Studies have shown that as occlusion increases, the ability to process visual movement, or ► [optic flow](#), deteriorates by having participants catch tennis balls while wearing spectacles that provided ► [vision](#) at specific frequencies. As the duration of occlusion increases, it becomes difficult for people to process the ► [perception](#) of ball movement accurately (Elliott et al. 1994).

## Cross-References

- [Animal Welfare](#)
- [Death](#)
- [Dentition](#)
- [Hippocampus](#)
- [Hypothalamus](#)
- [Optic Flow](#)
- [Perception](#)
- [Vision](#)

## References

- Ansari, S., Azari, H., McConnell, D. J., Afzal, A., & Mocco, J. (2011). Intraluminal middle cerebral artery occlusion (MCAO) model for ischemic stroke with laser doppler flowmetry guidance in mice. *JoVE (Journal of Visualized Experiments)*, 51, e2879–e2879.
- Casals, J. B., Pieri, N. C., Feitosa, M. L., Ercolin, A., Roballo, K., Barreto, R. S., Bressan, F. F., Martins, D. S., Miglino, M. A., & Ambrósio, C. E. (2011). The use of animal models for stroke research: a review. *Comparative Medicine*, 61(4), 305–313.
- Elliott, D., Zuberec, S., & Milgram, P. (1994). The effects of periodic visual occlusion on ball catching. *Journal of Motor Behavior*, 26(2), 113–122.
- Ferdinandy, P., Hausenloy, D. J., Heusch, G., Baxter, G. F., & Schulz, R. (2014). Interaction of risk factors, comorbidities, and comedications with ischemia/reperfusion injury and cardioprotection by preconditioning, postconditioning, and remote conditioning. *Pharmacological Reviews*, 66(4), 1142–1174.
- Fluri, F., Schuhmann, M. K., & Kleinschnitz, C. (2015). Animal models of ischemic stroke and their application in clinical research. *Drug Design, Development and Therapy*, 9, 3445.
- Jauch, E. C., Saver, J. L., Adams, H. P., Bruno, A., Demaerschalk, B. M., Khatri, P., McMullan, P. W., Qureshi, A. I., Rosenfield, K., Scott, P. A., Summers, D. R., Wang, D. Z., Wintermark, M., & Yonas, H. (2013). Guidelines for the early management of patients with acute ischemic stroke. *Stroke*, 44(3), 870–947.
- McCoy, G. (2013). Occlusion confusion. *General Dentistry*, 61(1), 71–75.
- Moshiri, A. (2015). Retinal artery occlusion. In *Handbook of vitreo-retinal disorder management: A practical reference guide* (p. 100). Toh Tuck Link, Singapore: World Scientific Publishing Co. Pte. Ltd.
- Mozaffarian, D., Benjamin, E. J., Go, A. S., Arnett, D. K., Blaha, M. J., Cushman, M., Das, S. R., Ferranti, S., Després, J., Fullerton, H. J., Howard, V. J., Huffman, M. D., Isasi, C. R., Jiménez, M. C., Judd, S. E., Kissela, B. M., Lichtman, J. H., Lisabeth, L. D., Liu, S., Mackey, R. H., Magid, D. J., McGuire, D. K., Mohler, E. R., Moy, C. S., Muntner, P., Mussolino, M. E., Nasir, K., Neumar, R. W., Nichol, G., Palaniappan, L., Pandey, D. K., Reeves, M. J., Rodriguez, C. J., Rosamond, W., Sorlie, P. D., Stein, J., Towfighi, A., Turan, T. N., Virani, S. S., Woo, D., Yeh, R. W., & Turner, M. B. (2016). Executive summary: Heart disease and stroke statistics-2016 update: A report from the American Heart Association. *Circulation*, 133(4), 447–454.
- Welch, W. H. (1899). *Thrombosis: Embolism*. London: Macmillan.

# N

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## Nerve Cells

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### Synonyms

[Neurons](#)

### Definition

Basic structural and functional unit of the nervous system.

### Introduction

Nerve cells or neurons are the signaling cells of the nervous system. They are involved in the generation of action potential and transmission of nerve impulses across the whole length of the body. Nerve cells are considered as the longest and oldest cell in one's body. Glial cells are the other cells (non-neuronal cells) in our brain, which provide support and protection to these nerve cells (Ganong 2005).

### General Structure

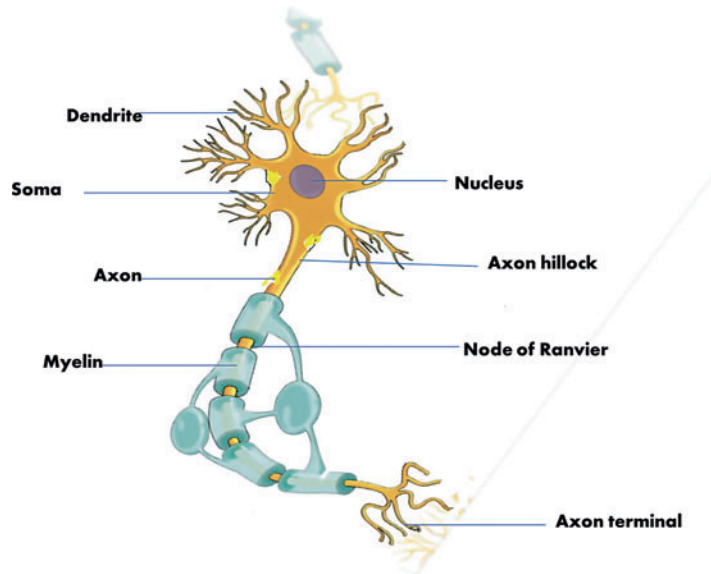
Nerve cells contain all the organelles of a general animal cell (like a nucleus, cell membrane, ribosomes, endoplasmic reticulum, Golgi apparatus, mitochondria, etc.). However, the specialized function of electrochemical signaling in nerve cells is provided by the presence of dendrites and axon, attached to the soma (or cell body) (Fig. 1). The cell body in human nervous system can measure from 10–100 micrometers in diameter. Dendrites are thin and short branch-like structures, whereas axon forms a long tail-like structure which originates from the soma at a swelled point known as axon hillock. Axon is covered by a protecting covering of myelin sheath, which is secreted by Schwann cells (a type of glial cell). Axon ends in numerous small terminal buttons. Nerve impulse moves from axon terminals of one neuron to the dendrite of another neuron via synapse (Baars and Gage 2010).

### Functions of Nerve Cells

Main function of nerve cell is to relay electrochemical signal from/to other cells in the body. The generation of action potential across the membrane of nerve cell is interplay of concentration gradient of sodium and potassium ions inside and outside of the cell. (For more information, see “► [Neural Impulse](#)”). The general nerve cells



**Nerve Cells, Fig. 1** Nerve cell (Image adapted from: [https://cnx.org/contents/GFy\\_h8cu@9.87:c9j4p0aj@3/Neurons-and-Glial-Cells](https://cnx.org/contents/GFy_h8cu@9.87:c9j4p0aj@3/Neurons-and-Glial-Cells))



send its signal by firing spikes from the cell body down to the axon to the terminal buttons. At the terminals, neurotransmitter is released from this nerve cell (presynaptic neuron) at synapse to trigger a postsynaptic potential in the next nerve cell (postsynaptic neuron) (Fig. 1) (de Robertis and de Robertis 2001). The connections of nerve cells and their pattern of interactions with each other are the major study points in cognitive neuroscience.

### Classification of Nerve Cells

Nerve cells have a great variety of shapes, branching patterns, and synapses. They can be classified into different ways:

- (a) On the basis of polarity:
  - (i) **Unipolar**: Axon or dendrite (either of them) emerges from the soma
  - (ii) **Pseudo unipolar**: Axon and dendrite emerge from the same side of soma
  - (iii) **Bipolar**: Axon and dendrite emerge from the opposite ends of soma
  - (iv) **Multipolar**: One axon and many dendrites emerge from the opposite ends of soma
- (b) On the basis of direction of neurotransmission:
  - (i) **Sensory**: conduct neurotransmission from tissues/organs to the brain, also known as afferent neurons
  - (ii) **Motor**: conduct neurotransmission from brain to the tissues/organs, also known as efferent neurons
  - (iii) **Association**: Nerve cells which connects sensory and motor neurons, also known as interneurons
- (c) On the basis of their firing pattern:
  - (i) **Tonic**: constantly active in discharge pattern
  - (ii) **Phasic**: fire in bursts or phase
  - (iii) **Fast**: rapidly fire with a fast rate
- (d) On the basis of their neurotransmitter:
  - (i) **Glutamatergic**: produce glutamate
  - (ii) **GABAergic**: produce gamma amino butyric acid
  - (iii) **Cholinergic**: produce acetylcholine
  - (iv) **Dopaminergic**: produce dopamine
  - (v) **Serotonineric**: produce serotonin
- (e) On the basis of myelination:
  - (i) **Myelinated**: axon is covered by myelin sheath
  - (ii) **Nonmyelinated**: axon is not covered by myelin sheath

## Cross-References

- ▶ [Action Potentials](#)
- ▶ [Afferent and Efferent Impulses](#)
- ▶ [Axon](#)
- ▶ [Cell Membrane](#)
- ▶ [Neural Impulse](#)
- ▶ [Neuron](#)
- ▶ [Neurotransmitters](#)
- ▶ [Synapse](#)

## References

- Baars, B. J., & Gage, N. M. (2010). Neurons and their connections. In *Cognition, brain, and consciousness* (pp. 63–69). Burlington: Academic.
- Ganong, W. F. (2005). Excitable tissue: Nerve. In *Review of medical physiology* (pp. 51–60). Singapore: McGraw Hill.
- de Robertis, E. D. P., & de Robertis, E. M. F. (2001). Cellular and molecular neurobiology. In *Cell and molecular biology* (pp. 661–676). Philadelphia: Lippincott Williams & Wilkins.

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# C

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## Clever Hans

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### Definition

Hans was a famous German Orlov Trotter horse trained by his owner, Wilhelm von Osten, who claimed that the horse was able to perform a variety of cognitive tasks, including solving complex arithmetic operations, giving the time, showing knowledge about calendar dates, understanding German language, and so on. His ability aroused worldwide interest at the beginning of the twentieth century, gaining the appellation of Clever Hans (der Kluge Hans in German). Experimental research conducted by the psychologist Oskar Pfungst found that the horse had no particularly complex cognitive abilities, although he was extremely skilled at gathering and using information from the most subtle movements of the questioners to give the expected response. This effect, later known as the observer-expectancy effect, shows the importance of keeping a tight control in experimental research using whenever possible an automated presentation of stimulation and recording of responses and, whenever that is not possible, using what is called the double-blind experimental design in which neither the experimenter nor the subject knows what behavior is expected from the subject.

### Introduction

Wilhelm von Osten taught mathematics at a German gymnasium during the early twentieth century, and he was the proud owner of a Russian trotting horse. He tutored the horse for 4 years, teaching him how to solve complex arithmetic problems by means of tapping with his feet. Exhibition of the ability of the horse, named Hans, was given daily in a courtyard in the northern area of Berlin. No fee was ever charged for attending to the exhibition as the owner, W. von Osten, was convinced that he had developed a training method that would allow showing that the difference between animal and human minds was a question of degree rather than quality. The horse Hans was able to answer a variety of questions by tapping with his front legs, like the number of people in the audience wearing hats or the result of adding two fractions such as  $2/5 + 1/2$  by tapping first the numerator and then the denominator (9/10). He was claimed to master cardinal numbers up to 100 and ordinals at least up to 10. He was also claimed to be able to read in German, bring a piece of a particular color from a row of colored cloths, tell the time to the minute, recognize notes and music intervals, and select which tones should be eliminated in a sequence of notes to reach a pleasant sound. Hans seem to be the living proof of Darwin (1871, p. 85) assertion: “Nevertheless the difference in mind between man and the higher animals, great as it is, certainly is one of the degree and not of kind.”

The ability of Hans, the horse, was uncanny, and he was classified by experienced educators as having the cognitive development of a 13–14-year-old teenager. Goes without saying that the interest about this particular horse spread rapidly throughout the world leading to a flood of articles in newspapers and magazines, being one of the most cited the one published on October 2, 1904, in the *New York Times*, in which it was lightly concluded that an special commission of experts decided that the horse actually used the reason. The image of the horse appeared in postcards, liquor labels, and other commercial products. Men of the greatest knowledge and reputation, of unimpeachable honor, would approach skeptical to the horse abilities, leaving convinced that they were truthful. The respected zoologist and African traveler, C. G. Schillings, was convinced by the fact that the horse was able to respond to strangers in the master's absence, assuring that they have not made the slightest sign to guide Hans response. Spectators were counted by the thousand, and they included from trick trainers to horse fanciers, but none of them was able to discover any kind of signals that the owner could be given to the horse to solve the problems. The issue was taken so seriously that Professor Carl Stumpf, the director of the Psychological Institute of the University of Berlin, after a cursory inspection during the month of February, 1904, requested from Mr. von Osten in July to detail the method he used to instruct the horse, before finally recommending the appointment of an investigating commission on September 3, 1904.

### Von Osten's Training Method

The method used by Mr. von Osten to train the horse was indeed quite simple and resembles the behavioral shaping method described by Skinner (1951) years later as a method of training by which successive approximations toward a target behavior are reinforced. W. von Osten conducted arithmetic training by using different sets of wooden pins, a counting machine (abacus), a chart upon which were pasted the numbers from 1 to 100, and digits

cut in brass and suspended from a string. Pieces of bread and carrots were used as rewards.

The work started by placing a single wooden pin in front to the horse and commanding him: "Raise the foot, one!" while holding the animal foot to ensure that the horse was giving only one tap. Once "one" was learned, he used two pins and the same method to train "two" and the rest of numbers. Gradually, it was not necessary to hold the foot, or to point to the pins, using directly the question "how many pins are there?" and associating the numbers with the responses. Once Hans allegedly learned the numbers, the next step was to teach the animal de concept "and," that is, to teach the animal how to add. To teach the horse the concept of "and," von Osten would have somebody holding a large cloth before the horse, where the wooden pins usually were placed. The cloth would be then taken up while pronouncing emphatically the word "and." After this he would hide two of the pins behind the cloth. As a result of its previous instruction Hans would give two taps at the sight of the pins. The same procedure was repeated with three pins. The next step was to set five pins up, three of which were covered by the cloth. The horse would tap two times and von Osten would say "two." The cloth then will be raised, Hans will give three taps more, and the trainer will say with emphasis: "and three." The idea underlying this method was that the image of the five pins would be associated by the horse with the combined groups of two and three. The next step was to ask the question without aids, so that it could be shown that the horse had learned to add. The problems become gradually more complicated until Hans began to give solutions to new problems by himself, leading the master to believe that "he had succeed in inculcating the inner meaning of the number concepts and not merely an external association of memory images with certain movement responses" (Pfungst 1907/1911, p. 249).

Multiplication was taught to Hans by using the abacus. Von Osten would place two identical sets of balls (i.e., three balls), one in each extreme of the abacus, and would ask the horse for how many times three balls were there, expecting two taps, then asking "how many, therefore are two times three?" Six taps. The horse was supposed to learn the meaning of the word "times" by means of the

spatial separation of the groups, counting the number of groups and the number of balls in each group. Subtraction was taught by setting a given number of pins up (i.e., five), removing some of them (i.e., two) while saying emphatically “I take away, two minus. How many are still standing?” A similar procedure was used for division and for other arithmetic operations.

### The Hans-Commission

Following the recommendation of Professor Stumpf, a commission of 13 people was established with the goal of evaluating whether there was “involved in the feats of the horse of Mr. von Osten anything of the nature of tricks, that is, intentional influence or aid on the part of the questioner” (Pfungst 1907/1911, p. 117). The commission involved a variety of relevant people, including a circus manager, members of schoolboards, directors of Berlin Zoological Garden, physiologists, and the director of the Psychological Institute of Berlin and member of the Academy of Sciences, Professor Carl Stumpf.

The commission conducted a large number of tests in the two sessions that took place on the 11th and the 12th of September, 1904, trying to search for the trick that could explain the behavior of the horse. In many of those tests, von Osten was not present but on September 12, 1904 two sets of experiments were conducted in which von Osten was present in the set. In the first set of experiments, a different man questioned the horse, while von Osten was present, but outside Hans’s view. The first set of questions was solved by Hans with little errors. In the second set of questions there was another man, the Zoologist and African traveler, C. G. Schillings, whom asked the horse to tap a certain number in the absence of von Osten, left the set, and then the owner entered the room and asked the horse to perform some arithmetical operation with a number that he was not aware of which one it was. In those tests, the horse did not perform near as well as in the other. In most tests, the horse repeated the original number, rather than the operation he was asked to perform. However, there was a misunderstanding that lead

Schillings to say to the horse “you are to repeat this number for Mr. von Osten” in the first few trials so that the errors might appear to be the result of this request or at least left the possibility open for an inconclusive test.

After its careful investigation, on their report of September 12, 1904, taking in account the individual experiences of the members of the commission with the horse, the report provided by Professor Stumpf on the method of instruction, and the two sessions of exploration, the commission concluded that no tricks or aids of the traditional sort were being employed by Hans’s owner. In their report it is said “In spite of the most attentive observation, nothing in the way of movements or other forms of expression which might have served as a sign, could be discovered. (. . .) They are unanimously agreed that this much is certain: This is a case which appears in principle to differ from any hitherto discovered, and has nothing in common with training, in the usual sense of that word, and therefore is worthy of a serious and incisive investigation” (Pfungst 1907/1911, pp. 253–254). Not quite the conclusion that the press at the time actually published, but one that opened the door a further and more controlled research that was finally conducted by the psychologists O. Pfungst.

### Oskar Pfungst’s Study on Hans Accomplishments

Given that no usual trick was discovered by the commission, and following the recommendation of conducting a more incisive research about the abilities of clever Hans, Oskar Pfungst conducted a careful set of experiments with the goal of discovering the actual abilities of the horse. The experiments were conducted in the courtyard of the owner, and most of them were conducted by Pfungst himself, using carrot, bread, and occasionally a square of sugar as rewards.

O. Pfungst approached the research by using what he called two different procedures. The so-called procedure without knowledge was a procedure in which neither the questioner, not anybody in the audience knew the answer to the

question the animal was asked, for opposition to the procedure with knowledge, in which the questioner knew the answer to the problem. Applying these procedures to problems that could be solved by tapping involving numbers in cards, words in placards, computation, counting using the abacus, memory tests, calendar dates, and musical abilities, Pfungst (1907/1911) found that the mean percentage of correct responses in the procedure without knowledge was about 10%, while in the procedure with knowledge was about 90%. Auditory stimuli seem not to play a role, as the animal could not follow instructions given by a questioner that was hidden from the horse's sight by blinders. Similar results were obtained in those problems that Hans solved with movements of the head and in those that were solved by approaching objects.

As the horse failed to find the solution when that solution was unknown by the people present, and the horse needed to see the questioner to give a solution, it was concluded that the horse was using some aid that was unintentionally given by the questioner. Focusing the exploration in the questioner, Pfungst (1907/1911) found that the horse behavior was controlled by minimal movements of the head and trunk of the questioner. A slight bent of the head while leaning the trunk slightly forward made the horse begin to tap with his right foot. As soon as the horse reached the right number of taps, the questioner would make a slight upward jerk of the head and the horse will stop tapping. Once these movements were isolated, Oskar Pfungst reports that he was able to control horse's behavior voluntarily, so that the horse will start tapping and stop tapping whenever the proper movements were given by the Pfungst, regardless of the question asked. In fact, he was able to control the rate of tapping by varying the angle of the inclination of the body so that greater the inclination, the faster the tapping.

The conclusion was clear "All wonderful feats of counting and computation which were accomplished while thus experimenting with the horse are to be accredited, not to the horse, but to the questioner (. . .) Hans, however, was also a faithful mirror of all the errors of the questioner" (Pfungst 1907/1911, p. 142). The results of this study were

reported by Carl Stumpf on December 9, 1904, in which he says "The horse must have learned, in the course of the long period of problem-solving, to attend ever more closely, while tapping, to the slight changes in bodily posture with which the master unconsciously accompanied the steps of his own thought-processes, and to use these as closing signals. The motive for this direction and straining of attention was the regular reward in the form of carrots and bread, which attended it." This last statement seems a clear description of the role of discriminative stimuli in instrumental or operant conditioning, indeed.

## Conclusion

There are some essential lessons that any person interested in animal cognition and in science in general may learn from the story of Clever Hans. The first and perhaps the most obvious one is the need of applying the principle of parsimony or Morgan's Cannon in any study of animal behavior: "In no case is an animal activity to be interpreted in terms of higher psychological processes, if it can be fairly interpreted in terms of processes which stand lower in the scale of psychological evolution and development" (Morgan 1895/1903, p. 59). In many occasions we tend to anthropomorphize the animal, providing it with feelings and abilities that are essentially human. It is true that we humans might tend to do the contrary at the same time, rejecting the idea that animals may have abilities that traditionally have been thought human exclusive. In that sense, it is convenient to remember that Lloyd Morgan himself completed his principle with a sentence that is often ignored by saying that "To this, however, it should be added, lest the range of the principle be misunderstood, that the canon by no means excludes the interpretation of a particular activity in terms of the higher processes, if we already have independent evidence of the occurrence of these higher processes in the animal under observation" (Morgan 1895/1903, p. 59). This was not the case of Clever Hans, whom followed one of the perhaps more interesting features of evolution, the ability to find simple solutions for complex problems. Using the available stimuli unconsciously provided by the



caretaker as discriminative stimuli for when an operant behavior would be followed by a reward was the simplest and most efficient and straightforward solution for a set of complex problems.

The second lesson that may be learned from the story of Clever Hans perhaps is not so obvious. An interesting question that is not usually raised is what led people of the beginning of the twentieth century to take so much trouble to study Hans's behavior. Even when the so-called Hans commission concluded that there were no obvious tricks of any sort in von Osten's behavior, the research was taken a step forward, and a systematic study was pursued. Of course, that is the way it should be done. But the question is would such a in-deep study have been conducted if there were not being a preconception about the (lack of) ability of the horse? In other words, would the same question had been applied when considering an ability that would fit the preconceptions about the species, regardless of whether they are true or not? These questions have no other goal that highlighting the need of applying Morgan's cannon to any situation, regardless of the species involved, keeping in mind that solving a problem by simple means does not necessarily implies that the species is not able of more complex cognition but simply that the animal is not applying it to solve that specific problem.

Third, as stated above, the story of Clever Hans makes it evident the importance of using proper controls when studying cognition regardless of the species to avoid the observer-expectancy effect, an effect in which the experimenter unconsciously influences behavior of the participant in a given experiment. This effect is usually controlled by using automatic recordings of behavior and by the use of the double-blind experimental design in which neither the experimenter nor the participant know the condition in which the participant are, not the behavior it is expected from him or her. This was essentially the method used O. Pfungst to explore Hans cognitive allegedly abilities.

Finally, the way the story of Clever Hans one may tend to question whether the horse actually deserved his nickname. When the research conducted by O. Pfungst showed that Hans did not have the abilities his master ascribed to him, Von Osten was both puzzled and deceived,

showing a reaction that was described by O. Stumpf as "genuine surprise, such a tragicomic rage directed against the horse" (Pfungst 1907/1911, p. 13), and explicitly forbid to conduct further experiments with him. It is easy to understand and even to share von Osten's disappointment. However, the story may be seen from a different point of view. In the story of Clever Hans, it is implicitly assumed that the problems the horse had to face were complex cognitive problems. But let's put ourselves in the horse's shoes. The only problem Hans had to solve was how to get the piece of carrot that his master provided when he tapped the right number of times. The key of the solution was the rule that determined which number was right. Von Osten established a complex set of rules for determining the correct number of tapings consciously and just one unconsciously. This latter one was the one used by Clever Hans. It was so subtle that a commission formed by 13 intelligent, motivated, and highly trained people was not able to discover the rule after two days searching for it. No wonder that Hans has kept the appellative of "clever" over a century.

## Cross-References

- ▶ [Associative Learning](#)
- ▶ [Double-Blind Experimental Design](#)
- ▶ [Instrumental Learning](#)
- ▶ [Morgan's Cannon](#)
- ▶ [Observer-Expectancy Effect](#)

## References

- Darwin, C. R. (1871). *The descent of man and selection in relation to sex*. London: Murray.
- Morgan, C. L. L. (1895/1903). *An introduction to comparative psychology (second edition, revised)*. London: Walter Scott Publishing.
- Pfungst, O. (1907/1911). *Clever Hans (the horse of Mr von Osten): A contribution to experimental animal and human psychology*. New York: Henry Holt and Company.
- Skinner, B. F. (1951). How to teach animals. *Scientific American*, 185, 26–29. doi:10.1038/scientificamerican1251-26.

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# D

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## Dishabituation

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### Definition

Dishabituation is defined as the immediate restoration of responding to a habituated stimulus that follows the presentation of a non-habituated stimulus.

### Introduction

The term habituation is used to describe the decremental effect of repeated presentations of the same stimulus upon the reflex response that this stimulus originally elicited. Habituation has been reported in a wide range of organisms, from single-celled animals to primates (Tighe and Leaton 1976). Once responding to a stimulus is habituated, presentation of a different stimulus right before presenting the stimulus that is already habituated results in a restoration of the habituated response to the original stimulus that it is called dishabituation (Thompson and Spencer 1966). The dishabituation phenomenon is one of the phenomena that allows for differentiating habituation from other decremental processes of behavior unrelated to learning such as fatigue.

Thus, dishabituation is found as a recovery of responding to a habituated stimulus as a consequence of presenting a new, different stimulus before the presentation of the original one. The amount of dishabituation decreases upon repeated presentations of the dishabituating stimulus in a phenomenon called habituation of dishabituation (Thompson and Spencer 1966). The fact that dishabituation disappears when the dishabituating stimulus habituates suggests that the dishabituating stimulus should be somehow unexpected and that it loses its power as novelty disappears (Rankin et al. 2009). Traditionally, the stimulus used to produce dishabituation has been a strong one, though some reports in the literature show that at least in some cases the use of a weak stimulus may play even a better role as a dishabituating stimulus than a strong one (Marcus et al. 1988).

### Theoretical Approaches

Dishabituation has been traditionally explained within the framework of the dual-process theory of habituation (Groves and Thompson 1970; Thompson 2009). This theory assumes that two independent processes underlie responding to repeated stimulus presentations: A habituation process affecting the reflex-arch that mediates response decrements, and a sensitization process affecting the general state of the organism that mediates response increments. These two

processes combine to produce the observed behavior. Dual-process theory of habituation suggests that dishabituation is caused by the superposition of an increase of a general responsiveness of the organism produced by the added stimulus (sensitization) that does not disrupt the process of habituation to the original stimulus, but reduces the general threshold for responding, facilitating the observation of the habituated response to the original stimulus.

The interpretation of dishabituation as an independent facilitation superimposed upon habituation suggested by the dual-process theory of habituation has accrued an important support over years of research in both, human (e.g., Kaplan and Werner 1986) and nonhuman animals (e.g., Carew et al. 1971; Kandel 1976). However, recent research seems to suggest that, at least within the field of the electrodermal orienting reflex in humans, dishabituation may also involve a disruption of the habituation process, with magnitude determined by the current arousal level (Steiner and Barry 2014). This is in agreement with the idea that dishabituation being considered as a disturbance of the habituation process as suggested by Sokolov (1963) in his neural-model comparator theory. However, these isolated results do not compromise the idea that, in general terms, dishabituation is due to the sensitization produced by presentation of the new stimulus rather than by a disruption of the habituation process that seems to remain intact in most cases.

## Conclusion

Dishabituation, understood as the response recovery from habituation that follows the presentation of a non-habituated stimulus (dishabituation) is a broad phenomenon found in a wide range of species, and it seems generally due to the non-habituated stimulus increasing the general level of arousal of the organism (sensitization).

## Cross-References

- ▶ [Habituation](#)
- ▶ [Sensitization](#)

## References

- Carew, T. J., Castellucci, V. F., & Kandel, E. R. (1971). An analysis of dishabituation and sensitization of the gill-withdrawal reflex in *Aplysia*. *International Journal of Neuroscience*, 2, 79–98. doi:[10.3109/00207457109146995](https://doi.org/10.3109/00207457109146995).
- Groves, P. M., & Thompson, R. F. (1970). Habituation: A dual-process theory. *Psychological Review*, 77, 419–450. doi:[10.1037/h0029810](https://doi.org/10.1037/h0029810).
- Kandel, E. (1976). *A cellular basis of behavior: An introduction to invertebrate neurobiology*. San Francisco: Freeman.
- Kaplan, P. S., & Werner, J. S. (1986). Habituation, response to novelty, and dishabituation in human infants: Tests of a dual-process theory of visual attention. *Journal of Experimental Child Psychology*, 42, 199–217. doi:[10.1016/0022-0965\(86\)90023-8](https://doi.org/10.1016/0022-0965(86)90023-8).
- Marcus, E. A., Nolen, T. G., Rankin, C. H., & Carew, T. J. (1988). Behavioral dissociation of dishabituation, sensitization, and inhibition in *Aplysia*. *Science*, 241 (4862), 210–213. doi:[10.1126/science.3388032](https://doi.org/10.1126/science.3388032).
- Rankin, H., et al. (2009). Habituation revisited: An updated and revised description of the behavioral characteristics of habituation. *Neurobiology of Learning and Memory*, 92, 135–138. doi:[10.1016/j.nlm.2008.09.012](https://doi.org/10.1016/j.nlm.2008.09.012).
- Sokolov, E. N. (1963). *Perception and the conditioned reflex*. London: Pergamon Press.
- Steiner, G. Z., & Barry, R. J. (2014). The mechanism of dishabituation. *Frontiers in Integrative Neuroscience*, 8, 14. doi:[10.3389/fnint.2014.00014](https://doi.org/10.3389/fnint.2014.00014).
- Thompson, R. F. (2009). Habituation: A history. *Neurobiology of Learning and Memory*, 92, 127–134. doi:[10.1016/j.nlm.2008.07.011](https://doi.org/10.1016/j.nlm.2008.07.011).
- Thompson, R. F., & Spencer, W. A. (1966). Habituation: A model phenomenon for the study of neuronal substrates of behavior. *Psychological Review*, 73, 16–43. doi:[10.1037/h0022681](https://doi.org/10.1037/h0022681).
- Tighe, R. J., & Leaton, R. N. (Eds.). (1976). *Habituation. Perspectives from child development, animal behavior, and neurophysiology*. New York: Lawrence Erlbaum Associates.

# D

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## Delay of Reinforcement

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### Keywords

Delay discounting; Response acquisition;  
Response maintenance

### Definition

*Delay of reinforcement* occurs when a period of time has elapsed between the response and the administration of the reinforcer.

Reinforcement is defined as the presentation or removal of a stimulus following an organism's response that results in an increased probability that the response will reoccur. For example, when a rat presses a lever and receives food, the rat learns that pressing the lever produces a desired result (food). The presentation of food (the reinforcer) increases the likelihood that the rat will press the lever again in the future. There are a number of factors that impact the efficacy of reinforcement, one of which is the delay of reinforcement. *Delay of reinforcement* occurs when a period of time has elapsed between the response and the administration of the reinforcer. For example, if a rat presses a lever that instantly releases food, the rat receives immediate reinforcement

since no time has elapsed between the response and the reinforcement. The passing of any time between the lever press and the delivery of food would qualify as delayed reinforcement.

### Parameters of Delayed Reinforcement

There are several important parameters of delayed reinforcement. One parameter of delay of reinforcement is the contiguity between the stimulus and the reinforcement. As the delay of reinforcement increases, the contingency decreases, thus leading to a reduction in the response rate. An immediately reinforced response leads to a strong association between the target response and the contingency (i.e., the reinforcer). When reinforcement is delayed, there is a weak association between the target response and the reinforcer. Oftentimes the response(s) that precedes the reinforcer has a stronger association with the reinforcer than the target response, thereby decreasing the perception of a contingency between the target response and the reinforcer. However, very short delays (0.5–2 s) of reinforcement have been found to lead to similar response rates, if not higher response rates than immediate reinforcement (Dews 1981; Sizemore and Lattal 1978). A rat that is immediately reinforced for pressing a lever is not only more likely to press the lever in the future but also more likely to press it at a higher rate than a rat that is on a 10-second (s) delay of reinforcement.

In addition to contiguity, delayed reinforcement can be affected by the delays being fixed or variable. *Fixed delayed reinforcement* (Sizemore and Lattal 1977) requires that the amount of time between the response and the reinforcement stays constant throughout the experiment. Delay of reinforcement could be fixed at 10 s, meaning the organism will not receive the reinforcer until 10 s have elapsed following each response. *Variable delayed reinforcement* (Sizemore and Lattal 1977) allows the time between the response and the reinforcement to potentially vary across trials. Variable delayed reinforcement of 10 s means the average elapsed time across all trials is 10 s; however, one trial of delayed reinforcement could involve a 1-s delay, while another trial could involve a 19-s delay.

Another parameter of delayed reinforcement is whether the delay is signaled or unsignaled. A *signaled delay of reinforcement* (Ferster and Skinner 1957) involves the presentation of an additional stimulus to indicate a delay period preceding reinforcement. Take a pigeon that is on a 10-s delayed schedule of reinforcement for pecking a green light when it is presented. In a typical signaled delay of reinforcement study, the pigeon will peck the green light, the cage will be blacked out during the delay (the signal is the blackout), and the pigeon will receive the reinforcer after the 10-s have elapsed. A signaled delay of reinforcement can be understood as a chain schedule because it presents an additional stimulus during the delay period, thereby creating a chain of stimuli. An *unsignaled delay of reinforcement* (Ferster and Skinner 1957) is when a delay period is not preceded by additional stimuli to indicate its onset. In the aforementioned example, the pigeon would not experience the blackout; rather, only the stimuli that were presented before the pigeon pecked the light would be present after the pecking response. An unsignaled delay of reinforcement can be conceptualized as a tandem schedule, which means that each component (i.e., stimulus, response, delay, and reinforcement) follows another.

A fourth parameter of delayed reinforcement is the occurrence of a superfluous response during the delay of the reinforcer. A response during the

delay period may cause the organism to be penalized, resulting in the restarting of the delay period. This is known as a *resetting delay* (Lattal 1987). In a 10-s resetting delay, a pigeon that pecks the green light within that 10-s delay period will cause the delay period to restart. The pigeon must not respond during the 10-s delay in order to receive the reinforcer at the end of the delay. A *non-resetting delay*, on the other hand, will not be affected by a response during the delay period (Lattal 1987). Once the organism has made the reinforcing response, any responses that occur during the delay period will have no effect on reinforcement.

### Efficacy of Delayed Reinforcement

The ability to continue engaging in behaviors that are maintained by delayed reinforcement is often difficult. Organisms are more likely to engage in immediately reinforced behaviors than behaviors that are reinforced after a delay period. For example, many individuals struggle to not eat the last piece of pie (immediate reinforcement) despite knowing the health benefits of refraining from doing so (delayed reinforcement). The ability to choose long-term benefits over short-term benefits is directly related to the concept of *delay discounting* (Mazur 2013). Delay discounting is the tendency to devalue a reinforcer as the delay of obtaining it increases, thereby leading individuals to place greater emphasis on smaller immediate reinforcers (a piece of pie) over larger delayed reinforcers (health). Delay discounting is an important concept for understanding self-control in humans because it points to the propensity for immediate rewards (piece of pie) over those delayed rewards that often take time to obtain (a healthy lifestyle).

To further understand delay discounting, it is important to understand how preferences toward immediate rewards over larger delayed reinforcers shift as a function of time. For instance, let's assume that a sweepstakes provides the option of choosing between a lump sum of \$10,000 in a year or choosing \$5,000 now. The choice of waiting a year for the \$10,000 seems like a much

more lucrative option. Now imagine that instead of \$5,000 now, the sweepstakes provides the option of choosing between a lump sum of \$10,000 in a year or choosing \$8,500 now. The preference of originally waiting a year (larger delayed reinforcer) for the \$10,000 has now shifted to perhaps accepting the \$8,500 now (immediate reinforcer). This is what is referred to as the indifference point. An *indifference point* is when the delay and the amount/value of the reinforcer are considered equally preferable; in this example that point is the \$8,500. This can result in the preference switching between the two options; thus, there are moments when the same individual may actually choose the larger delayed reinforcer (health) over the immediate reward (piece of pie), but there are also moments when the reverse is true.

The *Ainslie-Rachlin Theory* explains how the value of a reinforcer is discounted as a function of the amount of time that passes between the choice and receipt of the reinforcer (Ainslie 1975; Rachlin 1974). Specifically, the first assumption of the theory indicates that as the delay between making the choice and receiving the reinforcer increases, the value of the reinforcer decreases. The second assumption states that, at decision time, the reinforcer with the *highest* value will always be chosen. Therefore, despite the high value of a larger reinforcer (health), the delay of the reinforcer ultimately reduces the value that one places on their health. Moreover, when the individual is required to make a choice, the value of the piece of pie (immediate reinforcer) has significantly increased because of its close proximity. In the end, the piece of pie is considered greater than that of the healthy lifestyle. This line of research has helped explain impulsive choices that are often tied to maladaptive behaviors, such as drug/alcohol addiction.

The efficacy of delayed reinforcement depends on a variety of factors. Delayed reinforcement can decrease a behavior, increase a behavior, or leave the response rate unchanged. One factor that impacts its effectiveness is the purpose of delayed reinforcement. Delayed reinforcement is *primarily* used to maintain a response, also known as *response persistence* or *response maintenance*

(Lattal 2010). Most studies involving delay of reinforcement examine the effects of the delay on response persistence, whereby a steady response rate was initially obtained via a schedule of immediate reinforcement. Another possible aim of delayed reinforcement is *response acquisition*. Here, delayed reinforcement is used to foster a response despite the absence of a learning history.

The length of the delay period preceding the presentation of the reinforcer is another factor that influences the efficacy of delayed reinforcement. In examining response acquisition, Skinner (1953) found that he was not able to condition a pigeon to peck a key with a 10-s delay preceding reinforcement, but he was able to do so with immediate reinforcement or a 1-s delay. This suggests that reinforcement following a 1-s delay was able to change a pigeon's behavior, but a 10-s delay was too long. Despite Skinner's observation, Lattal and Gleason (1990) found that they were able to shape rats' and pigeons' behaviors using a 30-s delay. Since then, the study has been replicated several times and has expanded to include different species, including humans. These works are important, as they demonstrate that delayed reinforcement can lead to response acquisition, even if it generally occurs at a slower rate than immediate reinforcement. In fact, a 0.5-s delay of reinforcement leads to higher rates of responding than immediate reinforcement. The ability to wait for a delayed reinforcement is very adaptive and useful for a species.

In terms of response maintenance, several studies have shown that as the delay of reinforcement increases (say from 1 to 10 s), the response rate decreases. An organism is less likely to perform the behavior that produces reinforcement when there is a larger delay preceding reinforcement. In addition, studies have repeatedly found that delay of reinforcement following a steady response engendered by immediate reinforcement produces a lower response rate than if the behavior was maintained by immediate reinforcement. In other words, while delay of reinforcement can maintain behavior, it is likely to result in a lower response rate. It is also important to understand that an increase in the delay of reinforcement will



produce more variation in responding, potentially interacting with the existing contingencies.

Signaled and unsignaled delays also affect the efficacy of delay of reinforcement. While unsignaled and signaled delays are both likely to result in response acquisition and persistence, signaled delays maintain a higher rate of responding; however, the response rates are still lower compared to immediate reinforcement. Similarly, resetting delays are more likely to lead to response acquisition than nonresetting delays, albeit at a lower response rate than immediate reinforcement.

## Conclusion

As mentioned above, there are two main functions of delayed reinforcement: response maintenance or response acquisition. The primary function of delayed reinforcement is response maintenance: to perpetuate a previously established behavior. Delayed reinforcement for this purpose is most commonly used when the response was previously established by immediate reinforcement. Contrary to previous beliefs, recent research has demonstrated that delayed reinforcement can also lead to response acquisition with a delay period as long as 30 s. In fact, 0.5-s delay was found to consistently produce higher rates of responding than immediate reinforcement.

Skinner and Thorndike were two of the first researchers to explore reinforcement. They believed that the behavior must be “closely followed by” the reinforcer in order for the behavior to be acquired. Although much research has been conducted on delayed reinforcement, it is still unclear how the phrase “followed closely by” should be operationalized. Part of the challenge lies in the dynamic relationships of the parameters of delayed reinforcement. The effect of delayed reinforcement on response acquisition and response maintenance varies with the different combinations of parameters. Current research is focusing on how to better predict the interactions of the parameters.

## Cross-References

- ▶ [B. F. Skinner](#)
- ▶ [Behaviorism](#)
- ▶ [Contiguity](#)
- ▶ [Contingency](#)
- ▶ [Delayed Gratification](#)
- ▶ [Learning](#)
- ▶ [Operant Conditioning](#)
- ▶ [Positive Reinforcement](#)
- ▶ [Reinforcement](#)
- ▶ [Schedules of Reinforcement](#)

## References

- Ainslie, G. (1975). Specious reward: A behavioral theory of impulsiveness and impulse control. *Psychological Bulletin*, *82*(4), 463.
- Dews, P. B. (1981). Effects of delay of reinforcement on the rate of steady-rate responding. In C. M. Bradshaw, E. Szabadi, & C. F. Lowe (Eds.), *Quantification of steady-state operant behavior* (pp. 215–229). Amsterdam: Elsevier.
- Ferster, C. B., & Skinner, B. F. (1957). *Schedules of reinforcement*. East Norwalk: Appleton-Century-Crofts.
- Lattal, K. A. (1987). Considerations in the experimental analysis of reinforcement delay. In M. L. Commons, J. Mazur, J. A. Nevin, & H. Rachlin (Eds.), *Quantitative studies of operant behavior: The effect of delay and of intervening events on reinforcement value* (pp. 107–123). New York: Erlbaum.
- Lattal, K. A. (2010). Delayed reinforcement of operant behavior. *Journal of the Experimental Analysis of Behavior*, *93*(1), 129–139.
- Lattal, K. A., & Gleeson, S. (1990). Response acquisition with delayed reinforcement. *Journal of Experimental Psychology: Animal Behavior Processes*, *16*(1), 27.
- Mazur, J. E. (2013). *Learning and behavior* (7th ed.). Boston: Pearson.
- Rachlin, H. (1974). Self-control. *Behaviorism*, *2*(1), 94–107.
- Sizemore, O. J., & Lattal, K. A. (1977). Dependency, temporal contiguity, and response-independent reinforcement. *Journal of the Experimental Analysis of Behavior*, *27*, 119–125.
- Sizemore, O. J., & Lattal, K. A. (1978). Unsignaled delay of reinforcement in variable-interval schedules. *Journal of General Psychology*, *14*, 279–295.
- Skinner, B. F. (1953). *Science and human behavior*. New York: MacMillan.

# S

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## Self-Injurious Behavior

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### Synonyms

[Deliberate self-harm](#); [Self-injury](#); [Self-mutilation](#)

### Definition

Self-injurious behavior (SIB) encompasses the act of intentional harm to one's body that can result in or have the capacity to cause organ or tissue damage (Sigafos et al. 2014). Self-injurious behavior consists of a series of repetitive responses that often has no obvious reinforcer (Tate and Baroff 1966). Self-injurious behavior does not account for various ritualized cultural practices like ear piercing. SIB can vary in severity and can be put in a spectrum depending on the extent of injury (House and Cercone-Keeney 2004). SIB is utilized by individuals to temporarily alleviate intense negative emotions. They may also express self-directed anger or may be a notion to seek help from others. Such behaviors may also help avoid suicidal ideation (Klonsky and Muehlenkamp 2007).

## Common Forms of SIB

Examples of SIB can include behaviors like skin picking, head punching/slapping, pica (eating inedible objects), teeth grinding, eye poking, trichotillomania (pulling out hair), self-cutting, self-pinching, lip chewing, nail removal, air swallowing, and self-poking in body openings like the anus and vagina. Among these, head banging is the most commonly found self-injurious behavior (Sigafos et al. 2014). It is imperative to bear in mind that other behaviors may be more common among various subpopulations.

### SIB Classification

SIB can be classified within four categories: stereotypic, major, compulsive, and impulsive.

#### Stereotypic SIB

Stereotypic SIB consists of behavior that is highly repetitive, fixed, rhythmic, and monotonous. It is often seen in individuals with autism and various congenital and developmental disorders. SIB behavior in these individuals is often exhibited as head banging, self-hitting, skin picking, self-biting, and hair pulling (House and Cercone-Keeney 2004). Although pharmacologic treatment is slightly therapeutic for these individuals, behavioral interventions are much more effective in eliminating such behaviors.

### Major SIB

Major SIB includes single episodes of severe or life-threatening SIB. Examples include castration, eye gouging, and limb amputation. Such behaviors often times have significant meaning to the individual. Psychosis due to schizophrenia or a severe mood disorder are often related to major SIB (House and Cercone-Keeney 2004). The most common form of major SIB is genital mutilation; it is found at higher rates in men than in women. Antipsychotics are the recommended therapeutic pharmacologic treatment for major SIB (House and Cercone-Keeney 2004).

### Compulsive SIB

Compulsive SIB consists of repetitive, high-frequency behaviors that can be mild to moderately severe. These behaviors include trichotillomania, skin picking, and nail biting. Individuals find it difficult to resist such behaviors because they decrease tension or anxiety. Nail biting is the most common behavior in the general population and often times decreases in frequency over time. Behavioral treatments are effective in treating compulsive SIB. Medications can be taken simultaneously to therapeutically treat SIB (House and Cercone-Keeney 2004).

### Impulsive SIB

Impulsive SIB includes skin cutting, skin burning, and self-hitting. These behaviors temporarily relieve unbearable distress among individuals. Impulsive SIB is most commonly seen in those with borderline personality disorder. It is also seen in individuals with antisocial personality disorder, eating disorders, dissociative disorders, and post-traumatic stress disorder. Traumatic experiences can also trigger impulsive SIB. Data suggests that women are more likely to engage in impulsive SIB than men. Treatment includes adaptive strategies that replace the impulsive behavior to help cope with pain and emotions associated with trauma. Dialectical behavior therapy is effective in treating impulsive SIB in those who have borderline personality disorder. There is little data supporting effective pharmacological treatments at this time. (House and Cercone-Keeney 2004).

### SIB in Development

SIB is most commonly seen in adolescence and early adulthood. The age of onset is usually between ages 13 and 14. (Klonsky and Muehlenkamp 2007). SIB can also occur in early development between 2 and 3 years of age (Schroeder et al. 1997). Without proper treatment early in development, improvement of SIB is unlikely. SIB will often increase in severity during childhood and adolescence and will level out in adulthood (Emerson et al. 2001). Treatments for SIB will be likely throughout an individual's life.

### SIB Risk Factors

#### Disabilities

SIB is prevalent among individuals who have intellectual disabilities (Sigafos et al. 2014). Certain intellectual disabilities may increase the risk of SIB, further explaining its prevalence among this population (Holden and Gitlesen 2006; Lowe et al. 2007). SIB is even more prevalent in those individuals with intellectual disabilities as well as in those with autism or a psychological disorder like depression (Matson and LoVullo 2008). The prevalence of SIB increases with severe intellectual disabilities (Schroeder et al. 1997). SIB is seen more frequently in individuals who have severe disabilities in performing activities of daily living, socializing, and communicating (Emerson et al. 2001; Matson et al. 2000; Schroeder et al. 1997).

#### SIB Prevalence

Approximately 4% of adults report a past history of self-injury with up to 1% reporting a severe past history (Klonsky and Muehlenkamp 2007). Higher rates have been found in adolescents and in young adults, with even greater rates amongst those individuals receiving mental health treatment (Klonsky and Muehlenkamp 2007).

#### Gender and Ethnicity

SIB is found at similar rates amongst men and women. The methods of SIB vary between genders. Women are more likely to self-cut whereas

men are more likely to self-burn. Caucasian individuals are more likely to have SIB than its non-Caucasian counterparts (Whitlock et al. 2006).

## Why Individuals Engage in SIB

Affect regulation: SIB aid in alleviating intense negative emotion. Anger, anxiety, and frustration are present before initiating SIB, and a sense of calm immediately follows after injury. Self-punishment can also motivate SIB when the individual has low self-esteem. Although not as common, the urge to influence others may motivate SIB. Those engaging in SIB may feel antidissociation. These individuals explain that they often feel very little or nothing at all. By engaging in SIB, they are able to regain their sense of self (Klonsky and Muehlenkamp 2007). Some may use SIB to avoid attempting suicide. Other individuals may use SIB to seek excitement or exhilaration similar to those experienced during sky-diving or bungee jumping. Some individuals may use SIB to create physical boundaries, differentiating the individual from its environment and other people around him or her (Klonsky and Muehlenkamp 2007).

## Impacts of SIB

Treatment is imperative for individuals with SIB due to high risk of injury and health complications. Long-term health consequences can develop by accumulating damaged tissue over time. These individuals also will have increased medication use, isolation, and use of restraints to prevent SIB. Treatment can also be very expensive due to repetitive hospitalizations and medical care. (National Institutes of Health 1989). Negative social implications of SIB include isolation, difficulty assimilating into society, and maintaining employment. Likewise, there is a considerable strain in relationships between the individual with SIB and his or her parents, educators, and members of the community. This may significantly decrease overall quality of life for the individual with SIB (Rojahn et al. 2008).

## Treatment Options

Effective treatment includes those based on principles of applied behavior analysis (ABA) as well as those based on principles of behavior modification through environment manipulation. ABA treatment involves a two-step approach that uses assessments to identify the operant function of SIB and then implementing a treatment that will directly reduce SIB. Examples of ABA-based treatments include functional communication training (FCT), noncontingent reinforcement (NCR), and function-based extinction (FBE). Behavior modification treatments involve manipulation of the environment through reinforcement and/or punishment schedules without prior identification of SIB variables. Examples of behavior modification treatments include differential reinforcement schedules, punishment procedures, and contingent use of restraints (Scotti et al. 1991). Other treatment options include cognitive behavioral therapy, auditory integration training, sensory integrative therapy, weighted vests, gentle teaching, electroconvulsive therapy, and exercise. Although these treatment options are available, further research is required to determine their effectiveness. A combination of ABA and behavior modification is often recommended for SIB (Sigafoos et al. 2014).

Currently, there is no research that supports the use of pharmacologic treatment as an effective treatment independently. However, the use of pharmacologic agents can effectively treat symptoms of mental disorders that are often experienced in those individuals with SIB.

## Cross-References

- ▶ [Avoidance](#)
- ▶ [Behaviorism](#)
- ▶ [Conditioned Inhibition](#)
- ▶ [Conditioned Response](#)
- ▶ [Conditioned Stimulus](#)
- ▶ [Extinction in Learning](#)
- ▶ [Goal-Directed Behavior](#)
- ▶ [Negative Reinforcement](#)
- ▶ [Operant Conditioning](#)

- ▶ Positive Reinforcement
- ▶ Punishment
- ▶ Reinforcement

## References

- Emerson, E., Kiernan, C., Alborz, A., Reeves, D., Mason, H., Swarbrick, R., et al. (2001). The prevalence of challenging behaviors: A total population study. *Research in Developmental Disabilities, 22*, 77–93.
- Holden, B., & Gitlesen, J. P. (2006). A total population study of challenging behavior in the county of Hedmark, Norway: Prevalence and risk markers. *Research in Developmental Disabilities, 27*, 456–465.
- House, A. S., & Cercone-Keeney, J. (2004). Self-injurious behavior. In *Encyclopedia of women's health* (pp. 1177–1179). New York: Springer.
- Klonsky, D. E., & Muehlenkamp, J. J. (2007). Self-injury: A research review for the practitioner. *Journal of Clinical Psychology, 63*(11), 1045–1056.
- Lowe, K., Allen, D., Jones, E., Brophy, S., Moore, K., & James, W. (2007). Challenging behaviours: Prevalence and topographies. *Journal of Intellectual Disability Research, 51*, 625–636.
- Matson, J. L., & LoVullo, S. V. (2008). A review of behavioral treatments for self-injurious behaviors of persons with autism spectrum disorders. *Behavior Modification, 32*, 61–76.
- Matson, J. L., Anderson, S. J., & Bamburg, J. W. (2000). The relationship of social skills to psychopathology for individuals with mild and moderate mental retardation. *British Journal of Developmental Disabilities, 46*, 15–22.
- National Institutes of Health. (1989). *Treatment of destructive behaviors in persons with developmental disabilities, Consensus development conference statement* (Vol. 7(9)). Bethesda: National Institutes of Health.
- Rojahn, J., Schroeder, S. R., & Hoch, T. A. (2008). *Self-injurious behavior in intellectual disability*. Oxford: Elsevier.
- Schroeder, S. R., Tessel, R. E., Loupe, P. S., & Stodgell, C. J. (1997). Severe behavior problems among people with developmental disabilities. In W. E. MacLean Jr. (Ed.), *Ellis' handbook of mental deficiency, psychological theory and research* (3rd ed., pp. 439–464). Mahwah: Lawrence Erlbaum.
- Scotti, J. R., Evans, I. M., Meyer, L. H., & Walker, P. (1991). A meta-analysis of intervention research with problem behavior: Treatment integrity and standards of practice. *American Journal on Mental Retardation, 96*, 233–256.
- Sigafoos, J., O'Reilly, M. F., Lancioni, G. E., Lang, R., & Didden, R. (2014). In P. Sturmey & R. Didden (Eds.). *Self-injurious behavior; in evidence-based practice and intellectual disabilities*. Chichester: John Wiley & Sons, Ltd.,. doi: 10.1002/9781118326077.ch6.
- Tate, B. G., & Baroff, G. S. (1966). Aversive control of self-injurious behavior in a psychotic boy. *Behaviour Research and Therapy, 4*, 281–287.
- Whitlock, J., Eckenrode, J., & Silverman, D. (2006). Self-injurious behaviors in a college population. *Pediatrics, 117*, 1939–1948.

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## The Hyoid Bone

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### Synonyms

[Lingual bone](#); [Tongue bone](#)

### Definition

Unpaired, irregular, horseshoe-shaped bone that forms the attachment for the tongue suspends the larynx and assists in respiration, swallowing, and posture.

### Introduction

The hyoid bone is an irregular bone due to its unique quality of not articulating with any bones, rather connecting to other adjacent bones via muscles and tendons. It forms the attachment for the tongue and suspends the larynx, although not considered to be a part of the larynx itself. This unpaired bone provides attachment for numerous muscles, which function to either elevate or depress the hyoid bone, as well as assist the body in swallowing. In addition, these muscles

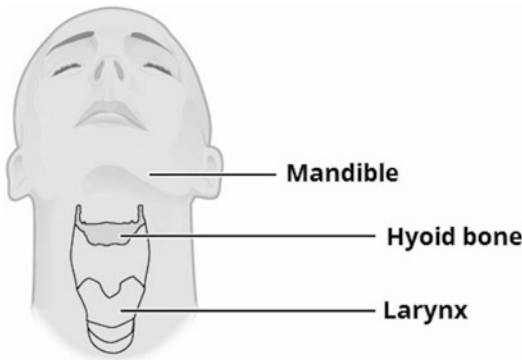
also help to support the hyoid itself, so that it is able to maintain its position. However, its exact position differs due to individual differences and situational circumstances within these individuals (Gray and Carter 2013; Ferrand 2013; Seikel et al. 2005).

### Anatomical Location and Structure

The hyoid bone is found superior to the larynx, inferior to the mandible, and anterior to the upper cervical vertebrae. The specific level of cervical vertebrae (i.e., C1–7) in which it is anterior to is contingent upon the individual's age and changes throughout the lifespan. It is located at the level of C2 or C3 from birth to age two and then moves slightly from the lower half of C3 and the upper half of C4 in older children and adults. From a sagittal viewpoint, the distance between the hyoid and cervical vertebrae remains the same until around puberty, when the hyoid moves slightly anteriorly (Hudgins et al. 1997). Figure 1 below depicts the position of the hyoid bone in relation to the larynx and mandible.

The hyoid is open posteriorly, thus giving it a horseshoe-like shape. It is comprised of three major components: the body, pair of greater cornu, and pair of lesser cornu. The body, also called the corpus, is convex anteriorly and concave posteriorly. It is also the point of origin or insertion for several muscles. These three components can be found in Fig. 2.





**The Hyoid Bone, Fig. 1** Hyoid bone in relation to the larynx and mandible (Young et al. 2013)

The greater cornu, or horn, articulates with the body laterally and extends itself posteriorly toward the cervical vertebrae. The hyoglossus, a muscle of the tongue, attaches to its outer surface, and the thyrohyoid, an infrahyoid muscle (i.e., below the level of the hyoid), attaches to its lower border.

The lesser cornu, or horn, is a small, cone-shaped projection that sits on the junction of the greater cornu and body. The stylohyoid, a suprahyoid muscle, is attached to its apex (Gray and Carter 2013). Figure 2 below depicts the point of attachment for these muscles.

## Function

The hyoid functions as the necessary attachment of the muscles responsible for respiration, swallowing, and preventing regurgitation. Apart from this role as of anchoring muscles, the hyoid itself is responsible for balancing the head by moving synchronously along with it. That is, if the head moves posteriorly or anteriorly, the hyoid will move posteriorly or anteriorly, respectively. Additionally, when the head moves dorsally, the hyoid bone rises, and when the head moves ventrally, the hyoid bone lowers (Bibby and Preston 1981).

## Muscle Articulations

There are several muscles anchored by the hyoid that serve several respective functions. These muscles can be divided into two general groups: suprahyoid (i.e., above the level of the hyoid) and infrahyoid (i.e., below the level of the hyoid). The suprahyoid and infrahyoid muscles can be identified in Fig. 3.

The suprahyoid muscles consist of the digastric, stylohyoid, mylohyoid, and geniohyoid. Their primary function is to raise the hyoid bone and larynx. These muscles also play an intricate role in swallowing by helping to raise the tongue and depress the mandible during this process. Swallowing consists of two major parts. The first part is comprised of the food being shifted from the mouth into the pharynx, via the hyoid bone and tongue moving superiorly and anteriorly. This is made possible by the digastric, mylohyoid, and geniohyoid muscles. The second part is comprised of the food passing through the pharynx and the hyoid bone rising back to its original position. The digastric and stylohyoid complete the process of this elevation of the hyoid bone. In addition, these muscles also prevent food from coming back up into the mouth.

The infrahyoid muscles consist of the sternohyoid, thyrohyoid, and omohyoid. Their primary function is to depress the larynx and hyoid bone after they have been drawn up in the process of swallowing. Furthermore, the omohyoid is specifically useful for drawn-out inhales.

In addition to the suprahyoid and infrahyoid muscles, the muscles of the tongue also have attachments to the hyoid bone. These muscles consist of the geniohyoglossus, hyoglossus, chondroglossus, and styloglossus. The hyoid provides support for the tongue and attachment for these muscles (Gray and Carter 2013; Seikel et al. 2005).



Furthermore, the lesser horns ossify leading up to and during puberty, with the ends of these horns ossifying by age 30. Thus, the hyoid appears as a single bone by age 30, while appearing as two separate structures, the corpus and posterior cornus, in earlier ages (Turkmen et al. 2012, 2014).

## Abnormalities

Abnormalities in the hyoid bone itself are often found together with cleft lip, cleft palate, or Pierre Robin syndrome (Turkmen et al. 2012, 2014). In addition, abnormalities associated with muscle articulations to the hyoid bone can also cause pathologies. Ossification of the stylohyoid ligament, part of the stylohyoid muscle apparatus, causes Eagle's syndrome. This is marked by chronic throat pain and is due to tissue structures applying excess pressure to the stylohyoid (Baig et al. 2012). Additionally, abnormal positioning of the hyoid can lead to obstructive sleep apnea (OSA). OSA is due to a blockage of the pharynx by the tongue during sleep and leads to snoring or insufficient inhalation of oxygen (Gent et al. 2014).

## Fracturing

The hyoid is rarely fractured naturally or as a result of sport injury, due to its location inferior to the mandible, which conveniently provides the hyoid protection. However, if the hyoid is fractured, it is generally a result of strangulation. A fractured hyoid leads to great pain in speaking and swallowing, due to the tongue having several muscle attachments at the hyoid.

## Cross-References

- ▶ [Feline Communication](#)
- ▶ [Fetus](#)
- ▶ [Morphology](#)

## References

- Baig, S., Patil, N., & Considine, N. (2012). An unusual cause of recurrent throat pain – calcified stylohyoid ligament. *Journal of the College of Physicians and Surgeons Pakistan*, 22(4), 258–260.
- Bibby, R. E., & Preston, C. B. (1981). The hyoid triangle. *American Journal of Orthodontics*, 80(1), 92–97.
- Ferrand, C. T. (2013). *Speech science: An integrated approach to theory and clinical practice* (3rd ed.). Boston: Pearson. Print.
- Gent, P. R., Schorr, F., Eckert, D. J., Gebrim, E., Kayamori, F., Moriya, H. T., Malhotra, A., & Lorenzi-Filho, G. (2014). Upper airway collapsibility is associated with obesity and hyoid position. *Sleep*, 37(10), 1673–1678.
- Gray, H., & Carter, H. V. (2013). *Gray's anatomy*. New York: Barnes & Noble.
- Hudgins, P. A., Siegel, J., & Abramowsky, C. R. (1997). The normal pediatric larynx on CT and MR. *American Journal of Neuroradiology*, 18, 239–245.
- Seikel, J. A., King, D. W., & Drumright, D. G. (2005). *Anatomy & physiology for speech, language, and hearing* (3rd ed.). Clifton Park: Thomson Delmar Learning.
- Turkmen, S., Cansu, A., Turedi, S., Eryigit, U., Sahin, A., Gunduz, A., & Shavit, I. (2012). Age-dependent structural and radiological changes in the larynx. *Clinical Radiology*, 67, e22–e26.
- Turkmen, N., Bulent, E., Selcuk, Ç., Filiz, E., & Naci, Ü. (2014). Anatomical variation of hyoid bone: A case report. *A Journal of Clinical Medicine*, 9(3), 272–274.
- Young, K. A., Korol, O., Kruse, D. H., Poe, B., Wise, J. A., DeSaix, P., . . . Womble, M. (2013). Chapter 7: Axial Skeleton. In *OpenStax's Anatomy and Physiology*. Retrieved March 20, 2017., from <https://openstax.org/details/anatomy-and-physiology>

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## **Roles of Medial Prefrontal Cortex Activity in Human and Animal Social Learning**

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### **Established Functions of the Medial Prefrontal Cortex in Human and Nonhuman Animal Cognition**

Research over the last two decades has seen advancements in neuroimaging techniques that reveal functional specialization within the prefrontal cortex (PFC) of the brain. Evidence thus far has implicated the PFC as the brain region responsible for high-level behavioral regulation via inhibition, executive function, and facilitation of complex social behaviors. Activation in subregions of the PFC, such as the medial prefrontal cortex (mPFC), is found to correspond with measurements of higher-order cognitive processes critical for learning, including attentional processes, decision making, and working memory (Hoover and Vertes 2007). The mPFC has been studied predominantly in rodents and rhesus monkeys. Derived analogue models of the brain suggest that mPFC is both anatomically and functionally similar to the human dorsolateral PFC (Goodell et al. 2017).

While literature has thus far focused on the mPFC as a site associated with perceptual functioning, including attention and memory (Siddiqui et al. 2008), few discussions have explicated its role across social-cognitive development. Recently, emerging interests have led to the discovery of the mPFC's importance in social processing and learning. Both animal and human studies indicate that the mPFC is involved in moral reasoning, mentalizing, monitoring, and predicting others' behaviors as well as person perception. This review attempts to elucidate the role of the mPFC in guiding social learning and predicting positive and negative outcomes of others' actions (e.g., Apps and Sallett 2017) through examination and discussion of extant neuroimaging and neuropsychological findings across animal and human research. Directions for future research will also be presented, such as those that investigate the mPFC and related circuitry underlying emotional and social processing in both human and animals.

### **Initial Evidence for mPFC Role in Memory and Higher Cognitive Processes**

Interest in the mPFC region was previously limited to its relationship with the anterior cingulate cortex (ACC) in facilitating purely cognitive processes such as memory and attention, having little to no involvement with emotion processing or social behavior in both humans and animals. For

example, studies have shown involvement of the mPFC in short-term and long-term memory and more complex cognitive processing to aid in guiding behavior and decision making. Due to differences in methodology, research has produced inconsistent findings on the mPFC's contribution to cognition (Alexander and Brown 2011). These discrepancies in results impose challenges for theoretical models to explain the purpose of the ACC/mPFC relationship in higher-order functions. Some results show significant involvement of the mPFC in the motivational aspects of attention, error detection, learning from aversive outcomes, and executive functions (Apps and Sallet 2017).

Past studies have highlighted the role of mPFC in memory function through consistent results showing decreased performance on recall tasks when the mPFC was inhibited during learning (Euston et al. 2012). Results have suggested that the mPFC tracks "remote" memories consisting of information learned more than one week before the date of attempted retrieval (Takashima et al. 2006). Additionally, mPFC inactivation has been associated with impaired retention of fear-related memories when tested one day after exposure to fear stimuli, suggesting its role in "recent memory" formation. Still more studies show that mPFC interference immediately following a learning period inhibits later recall ability, pointing to the role of the mPFC in memory consolidation, i.e., long-term memory. In short-term memory, mPFC lesions lead to recall deficits for location-specific reward associations over delays of 30 min (Seamans et al. 1995). These results demonstrate the importance of mPFC activation in long- and short-term memory and recent and remote memory. However, more functional specializations in the mPFC have been found in recent studies, adding to the variety of functions carried out by this area.

Despite its overlap with memory functions, what differentiates the mPFC from other brain areas is its critical role in directing adaptive behavior (Euston et al. 2012). Evidence suggests that the mPFC uses the aforementioned memory systems to store and process contextual information to produce an adaptive response. Specifically,

combined electrophysiological and anatomical findings in rat studies indicate that the mPFC takes current contextual information to predict the most adaptive response in particular situations, based on remembered experiences (Euston et al. 2012). This forms a kind of behavioral feedback loop where the organism learns new adaptive behavioral responses based on the alignment of previous responses with environmental expectations and conditions (i.e., context).

Electrophysiological studies show divergent specializations pertaining to specific subregions of the mPFC, where the internal structure of this system can be divided on a dorsal-ventral gradient: Activity in the dorsal mPFC (including the infralimbic and ventral prelimbic cortex) appears to be strongly associated with musculoskeletal action, whereas activity in the ventral mPFC (including the dorsal prelimbic and anterior cingulate cortex) is more associated with reward-dependent outcomes, i.e., emotional control (Euston et al. 2012). Dorsal mPFC regions thus receive input from motor areas of the brain to produce adaptive action, and the ventral mPFC receives input from emotion-related brain regions, producing adaptive emotional responses based on reward contingencies. As such, the input/output differences occurring between the subdivisions of the dorsal/ventral mPFC gradient account for the processing of motivational stimuli on the one hand and control motor activity on the other.

To learn adaptive behavioral skills, the mPFC's feedback mechanism initially tracks contextually relevant environmental information that is motivationally salient with help from the hippocampus. The mPFC relies on the rapid associative functions of the hippocampus to learn from spatial and emotional cues quickly, as it binds associations between contexts, events, and responses (Hirel et al. 2013), helping the mPFC obtain maps of its inputs and outputs based on associations of motivationally salient cues. As associations become routine, the mPFC begins to store feedback information locally – independent of the hippocampus – in the form of schemata (Euston et al. 2012). This transition is largely due to memory consolidation, where memory is consolidated in the mPFC during periods of reactivation,

mirroring hippocampal “sharp waves” with high-density field potential oscillations (Euston et al. 2012; Johnson et al. 2010). Again, this is suggestive of the role long-term memory plays in mPFC functioning.

The learning of adaptive behavior as a result of mPFC functionality also extends to emotion regulation. For instance, the relationship between the mPFC and ACC is implicated in negative and positive emotion appraisal and expression (Etkin et al. 2011). mPFC connectivity with regions of the limbic system such as the amygdala, periaqueductal gray, and hypothalamus supports complex processing of emotional information via top-down processing. These connections form a network that supports working memory (Etkin et al. 2011) and serve as a basis for integrating emotional information into memory processing. Further studies demonstrate that greater activation in the ACC and mPFC is associated with the regulation and sensitivity of negative emotions (i.e., disgust), as well as the expression of negative emotions such as pain and empathic concern (Ochsner and Gross 2008). Extinction of fear and appetitive learning, as well as processing anger, activates the ventral and dorsal regions of the mPFC, respectively. These findings provide further support for the idea that intact mPFC connectivity to subcortical regions is fundamental to processing and responding to emotional stimuli in social contexts.

Prior studies on mPFC functionality provide evidence for a division of labor in emotion processing, where mPFC subregions work independently to regulate fear. Similar to the aforementioned anatomical division between motor- and reward-based input/output configurations, these emotion-oriented subregions include dorsal areas (prelimbic/dACC) which regulate fear expression and ventral areas (infralimbic/vmPFC) which regulate fear suppression (Giustino and Maren 2015). The body of research presented here demonstrates the importance of an intact mPFC in learning, memory, and emotion regulation, the latter being crucial for adaptive social behavior. It is thus important to understand how the mPFC is involved in different types of social learning, cognition, and behavior.

## mPFC Role in Social Cognition and Learning

Here, we refer to social learning as (a) the formation of emotional responses to others’ behaviors, facial expressions, and speech, (b) formation and maintenance of expectations about social environments, and (c) decision making processes related to social interactions. Recent studies have shown that the mPFC has been implicated in “processing, representing and integrating social and affective information” (Grossman 2013, p. 1). Additional studies demonstrating social learning processes in the mPFC involve self-reflection, person perception, and theory of mind/mentalizing (Amodio and Frith 2006), understanding self and others, decision making in adults (Heekeren et al. 2008), predicting others’ preferences (Kang et al. 2013), and learning and predicting the likely outcomes of actions of the self and others (Alexander and Brown 2011). Additionally, it has been demonstrated that the mPFC is implicated in facilitating coordination between animals, regulating social interactions, and carrying out complex defensive behaviors (Goodell et al. 2017).

In fact, functionality of the mPFC is implicated in social learning very early on in development. According to a review of infant studies on the PFC by Grossman (2013), mPFC lesions lead to anti-social behaviors such as interpersonal violence, vandalism, and stealing. In terms of moral reasoning, mPFC lesions lead to more utilitarian, ego-centric responses to moral dilemmas, decreased willingness to resolve interpersonal conflicts, and consideration of the consequences that behavior has on others and dysregulated autonomic responses to punishment (Grossman 2013). This pattern of results suggests that damage to the mPFC has severe consequences for social functioning; in terms of development, the mPFC seems to be less plastic than other areas of the brain (Thomas and Johnson 2008).

The formation of expectations in social situations is an important aspect for successful interpersonal attachments and relationships. In a speed-dating experiment with human participants, Cooper and colleagues (2014) found that expressions of interest in potential partners, as well as



feelings of rejection, were associated with increased activation in the posterior superior temporal sulcus and the rostromedial PFC. The mPFC specifically responded to prediction errors from the reinforcement-learning model of personal desirability, suggesting that predicting and expressing both desirability and rejection involve a quantitative calculation in neural networks responsible for processing social rewards (Cooper et al. 2014). This study provides further evidence for the role of the mPFC in forming social expectations that are informed by emotions.

The mPFC promotes the ability to monitor others' actions and detect errors in others' actions, an important factor in successfully responding to others in interpersonal interactions. In a study of two monkeys, Isoda (2017) found that when monitoring both the individual and the others' actions, differing neuronal populations in the mPFC coded divergently for actions pertaining to the individual versus actions pertaining to the other. When another monkey committed errors in its actions, mPFC neurons demonstrated a phasic increase in activity, suggesting that the mPFC is biased toward social information that would inform future expectations.

Neuroimaging findings in humans show that a newborn's mPFC activity significantly increases in response to a mother reading a book using infant-directed speech, as opposed to a mother reading in adult-directed speech. This suggests that the mPFC aids in motivating attention toward cues that are socially interactive (Saito et al. 2007). The mPFC might thus be involved in learning from others by detecting the relevance of others' actions with reference to the self.

Recent evidence highlights the mPFC's direct involvement in regulating aggressive behaviors. According to Goodell et al. (2017), aggression observed in rodents may be directly associated with changes in mPFC function due to post-weaning social isolation (PSI) may be directly related to aggression in rodents that were previously exposed to PSI. Intuitively this would make sense, as emotion regulation and executive functioning are both strongly related to mPFC functionality (Goodell et al. 2017). In addition, a decrease in executive functioning has previously

been linked to an increase in physical aggression, supporting the notion that mPFC functionality would be involved. Other studies linking mPFC abnormalities to PSI provide evidence for atypical changes in structure and function, including a dampened expression of early genes (Wall et al. 2012), dendritic spine morphology (Ferdman et al. 2007), and synaptic-related proteins such as PSD-95, a protein involved in synaptic plasticity, (Hermes et al. 2011). In a study using optogenetic stimulation, increased stimulation of the mPFC demonstrated a decrease in aggression in mice; optogenetic silencing, on the other hand, showed a marked increase of aggressive behaviors (Takahashi et al. 2014). Demonstrating increases of FOS (a family of genes responsible for regulating cell proliferation, transformation, and differentiation) in the prelimbic area (PL), results from Goodell et al. (2017) support previous findings that socially dominant mice expressed higher levels of the c-FOS gene in the PL subregion of the mPFC (Wang et al. 2011). Their results indicate an elevation in social rank when rodents interact with other nonaggressive rats, revealing mPFC functional sensitivity to the behavioral characteristics of stimulus rats. Finally, changes in PSD-95 punctae in the ventral mPFC of isolated rats with social learning differences indicated more time spent with aggressive stimulus rats. Their results insinuate that social isolation may play a causal role in the maintenance of abusive social behavior.

A few theoretical orientations have arisen from these results. According to the somatic marker hypothesis (Damasio 1996), information from the ventromedial PFC and orbitofrontal cortex contains somatic markers that allows learning by experience by linking experiential contingencies with previous emotional experience. For individuals with vmPFC damage or dysregulation, effectively utilizing context-appropriate somatic markers becomes difficult, resulting in behavior and cognition that appears similar to sociopathy (Siddiqui et al. 2008). mPFC dysfunction has also been implicated in other clinical disorders including schizophrenia, bipolar disorder, and autism spectrum disorder in which social impairment is a main characteristic (Goodell et al. 2017).

Both human and monkey fMRI studies demonstrate that learning to anticipate the value of actions and forming expectations about actions, as well as detecting unexpected outcomes, seem to be important processes aided by the mPFC. Alexander and Brown's (2011) theory and model of mPFC function referred to as the predicted response-outcome (PRO) model suggests that: "individual neurons generate signals reflecting a learned prediction of the probability and timing of the various possible outcomes of an action. These prediction signals are inhibited when the corresponding predicted outcome actually occurs. The resulting activity is therefore maximal when an expected outcome fails to occur, which suggests that mPFC signals in part the unexpected non-occurrence of a predicted outcome" (p. 2). Instead, it maps existing action plans in a stimulus context to predictions of the responses and outcomes that are likely to result, i.e., response-outcome learning. It allows multiple possible action outcomes to be predicted simultaneously, each with a corresponding probability (Alexander and Brown 2011).

As previously stated, the majority of research relating the mPFC to social cognition is based on studies examining the sulcus of the ACC – specifically, the sulcus of the ACC (ACCs) – and pertains to the ACCs's influence on reinforcement learning (Kolling et al. 2016). To recapitulate, reinforcement learning theory (RLT) states that the ACCs anticipate and monitor the value of behaviors by evaluating the differences between behavioral outcomes and expectations, yielding a prediction error (PE) (Apps and Sallet 2017). Impaired PE coding is strongly associated with impaired social cognition (Hill et al. 2016), as PEs inform future-oriented decision making, learning, and adaptive behavior. These recent findings mark the beginning of a social learning-focused model for mPFC function in which the avoidance and anticipation of social errors influence social behaviors. However, not much is known regarding more complex and specific social behaviors in humans.

A study conducted by Kumaran et al. (2016) provides new evidence for how social hierarchies, defined by status inference, are learned. The study

suggests that the degree of change in an individual's perception of social hierarchies fluctuate depending on whether they are self-relevant or not. In their study, participants were asked to differentiate the social status of individuals based on whether they belonged to either a "self-hierarchy" – the one to which individual participants themselves belonged to – or an "other-hierarchy," which included strangers, as well as acquaintances and close friends (Cikara and Gershman 2016). How much the participants' belief about social status changed due to feedback was associated with increased activation in the mPFC, amygdala, and hippocampus. According to Kumaran et al. (2016), these brain regions thus form the basis of a "social status inference engine," in which the mPFC pertained specifically to changes in belief regarding the self-hierarchy condition, i.e., when participants demonstrated a bias toward their own social status. This is corroborated by mPFC regions (including the pregenual anterior cingulate) that are correlated with thoughts about one's own personal traits, mental status, and characteristics (Jenkins and Mitchell 2011). The role of the mPFC is further supported by its designation for representing others who are characteristically similar to one's own traits. Kumaran et al.'s (2016) results highlight a condition where the mPFC is only able to make representations of others when the "self" is used as a diagnostic template (Cikara and Gershman 2016). In other words, the mPFC uses information that is self-referential when making judgments about others who exhibit similar traits. Self-referencing is not relevant when beliefs about a hierarchy pertain to another hierarchy; thus the mPFC only seems to code for the behavior of others when they are similar to one's own behavior (Cikara and Gershman 2016). These results support Festinger (1954), who established the idea that evaluations of self-referential behaviors are acquired via social comparisons with others that exude behavioral characteristics similar to one's own.

In sum, experimental data on human and non-human animals demonstrate the crucial role of the mPFC in social learning and cognition. We have established that the mPFC, due to its functional

connectivity to subcortical regions of the brain, informs social learning processes via emotional and motor inputs, error detection and predictions, and self-relevant information. The present review has demonstrated that the mPFC is important for far more complex social and emotional behaviors than purely higher-level cognitive/perceptual functions, as previously thought.

## Future Directions

The current review of the literature on the role of the mPFC in social learning suggests that more research focused on specifying the preference for varying types of social information in the mPFC is needed. In addition, there is a lack of research on mood and anxiety disorder-related effects on mPFC activation during social learning tasks. This type of research would help identify which components of social learning processes are affected by mPFC dysregulation caused by psychopathology. More research looking at the developmental pattern of mPFC activation during social cognition tasks would determine whether the role of the mPFC changes over time. In addition, continued mPFC neuroimaging research in clinical samples could inform treatment methods for patients diagnosed with various communication disorders and psychopathology. For example, transcranial magnetic stimulation of the mPFC modulates the processing of facial expressions in a priming task. Additional research in this vein, especially with clinical samples, could further our understanding of how social information, such as faces, are processed in clinical disorders and how TMS techniques can be applied to remediate dysfunctional information processing in the brain and positively affect emotional experiences of others.

In addition, several studies have been limited by possible confounding results stemming from overlapping brain areas. In some cases, it is unclear whether a lesion-based finding is the result of one distinct brain area or due to the effects of another overlapping area. Furthermore, it has been found that surrounding brain regions are able to compensate for loss in a proximally related region. Hence, more studies involving

single unit recordings and neuropsychological studies showing double dissociations that measure causal factors responsible for functional deficits due to neural abnormalities are needed.

## Cross-References

- ▶ [Amygdala](#)
- ▶ [Decision-Making](#)
- ▶ [Hippocampus](#)
- ▶ [Hypothalamus](#)
- ▶ [Long-Term Memory](#)
- ▶ [Short-Term Memory](#)
- ▶ [Social Learning](#)
- ▶ [Theory of Mind](#)
- ▶ [Top-Down Processing](#)
- ▶ [Working Memory](#)

## References

- Alexander, W. H., & Brown, J. W. (2011). Medial prefrontal cortex as an action-outcome predictor. *Nature Neuroscience*, *14*(10), 1338–1344.
- Amodio, D. M., & Frith, C. D. (2006). Meeting of minds: The medial frontal cortex and social cognition. *Nature Reviews Neuroscience*, *7*(4), 268–277.
- Apps, M. A., & Sallet, J. (2017). Social learning in the medial prefrontal cortex. *Trends in Cognitive Sciences*, *21*(3), 151–152.
- Cikara, M., & Gershman, S. J. (2016). Medial prefrontal cortex updates its status. *Neuron*, *92*(5), 937–939.
- Cooper, J. C., Dunne, S., Furey, T., & O’Doherty, J. P. (2014). The role of the posterior temporal and medial prefrontal cortices in mediating learning from romantic interest and rejection. *Cerebral Cortex*, *24*(9), 2502–2511.
- Damasio, A. R. (1996). The somatic marker hypothesis and the possible functions of the prefrontal cortex. *Philosophical Transactions of the Royal Society of London*, *351*, 1413–1420.
- Etkin, A., Egner, T., & Kalisch, R. (2011). Emotional processing in anterior cingulate and medial prefrontal cortex. *Trends in Cognitive Sciences*, *15*(2), 85–93.
- Euston, D. R., Gruber, A. J., & McNaughton, B. L. (2012). The role of medial prefrontal cortex in memory and decision making. *Neuron*, *76*(6), 1057–1070.
- Ferdman, N., Murmu, R. P., Bock, J., Braun, K., & Leshem, M. (2007). Weaning age, social isolation, and gender, interact to determine adult explorative and social behavior, and dendritic and spine morphology in prefrontal cortex of rats. *Behavioural Brain Research*, *180*(2), 174–182.

- Festinger, L. (1954). A theory of social comparison processes. *Human Relations*, 7(2), 117–140.
- Giustino, T. F., & Maren, S. (2015). The role of the medial prefrontal cortex in the conditioning and extinction of fear. *Frontiers in behavioral neuroscience*, 9, 298.
- Goodell, D. J., Ahern, M. A., Baynard, J., Wall, V. L., & Bland, S. T. (2017). A novel escapable social interaction test reveals that social behavior and mPFC activation during an escapable social encounter are altered by post-weaning social isolation and are dependent on the aggressiveness of the stimulus rat. *Behavioural Brain Research*, 317, 1–15.
- Grossmann, T. (2013). The role of medial prefrontal cortex in early social cognition. *Frontiers in Human Neuroscience*, 7, 340.
- Heekeren, H. R., Marrett, S., & Ungerleider, L. G. (2008). The neural systems that mediate human perceptual decision making. *Nature Reviews Neuroscience*, 9(6), 467–479.
- Hermes, G., Li, N., Duman, C., & Duman, R. (2011). Post-weaning chronic social isolation produces profound behavioral dysregulation with decreases in prefrontal cortex synaptic-associated protein expression in female rats. *Physiology & Behavior*, 104(2), 354–359.
- Hill, M. R., Boorman, E. D., & Fried, I. (2016). Observational learning computations in neurons of the human anterior cingulate cortex. *Nature Communications*, 7, 12722.
- Hirel, J., Gaussier, P., Quoy, M., Banquet, J. P., Save, E., & Poucet, B. (2013). The hippocampo-cortical loop: Spatio-temporal learning and goal-oriented planning in navigation. *Neural Networks*, 43, 8–21.
- Hoover, W. B., & Vertes, R. P. (2007). Anatomical analysis of afferent projections to the medial prefrontal cortex in the rat. *Brain Structure and Function*, 212(2), 149–179.
- Isoda, M. (2017). Self–other differentiation and monitoring others' actions in the medial prefrontal cortex of the monkey. In *The prefrontal cortex as an executive, emotional, and social brain* (pp. 151–167). Tokyo: Springer.
- Jenkins, A. C., & Mitchell, J. P. (2011). Medial prefrontal cortex subserves diverse forms of self-reflection. *Social Neuroscience*, 6(3), 211–218.
- Johnson, L. A., Euston, D. R., Tatsuno, M., & McNaughton, B. L. (2010). Stored-trace reactivation in rat prefrontal cortex is correlated with down-to-up state fluctuation density. *Journal of Neuroscience*, 30, 2650–2661.
- Kang, P., Lee, J., Sul, S., & Kim, H. (2013). Dorsomedial prefrontal cortex activity predicts the accuracy in estimating others' preferences. *Frontiers in Human Neuroscience*, 7, 686.
- Kolling, N., Behrens, T. E. J., Wittmann, M. K., & Rushworth, M. F. S. (2016). Multiple signals in anterior cingulate cortex. *Current Opinion in Neurobiology*, 37, 36–43.
- Kumaran, D., Banino, A., Blundell, C., Hassabis, D., & Dayan, P. (2016). Computations underlying social hierarchy learning: Distinct neural mechanisms for updating and representing self-relevant information. *Neuron*, 92(5), 1135–1147.
- Ochsner, K. N., & Gross, J. J. (2008). Cognitive emotion regulation: Insights from social cognitive and affective neuroscience. *Current Directions in Psychological Science*, 17(2), 153–158.
- Saito, Y., Aoyama, S., Kondo, T., Fukumoto, R., Konishi, N., Nakamura, K., & Toshima, T. (2007). Frontal cerebral blood flow change associated with infant-directed speech. *Archives of Disease in Childhood-Fetal and Neonatal Edition*, 92(2), F113–F116.
- Seamans, J. K., Floresco, S. B., & Phillips, A. G. (1995). Functional differences between the prelimbic and anterior cingulate regions of the rat prefrontal cortex. *Behavioral neuroscience*, 109(6), 1063.
- Siddiqui, S. V., Chatterjee, U., Kumar, D., Siddiqui, A., & Goyal, N. (2008). Neuropsychology of prefrontal cortex. *Indian Journal of Psychiatry*, 50(3), 202–208.
- Takahashi, A., Nagayasu, K., Nishitani, N., Kaneko, S., & Koide, T. (2014). Control of intermale aggression by medial prefrontal cortex activation in the mouse. *PLoS One*, 9(4), e94657.
- Takashima, A., Petersson, K. M., Rutters, F., Tendolkar, I., Jensen, O., Zwarts, M. J., . . . & Fernandez, G. (2006). Declarative memory consolidation in humans: a prospective functional magnetic resonance imaging study. *Proceedings of the National Academy of Sciences of the United States of America*, 103(3), 756–761.
- Thomas, M. S., & Johnson, M. H. (2008). New advances in understanding sensitive periods in brain development. *Current Directions in Psychological Science*, 17(1), 1–5.
- Wall, V. L., Fischer, E. K., & Bland, S. T. (2012). Isolation rearing attenuates social interaction-induced expression of immediate early gene protein products in the medial prefrontal cortex of male and female rats. *Physiology & Behavior*, 107(3), 440–450.
- Wang, F., Zhu, J., Zhu, H., Zhang, Q., Lin, Z., & Hu, H. (2011). Bidirectional control of social hierarchy by synaptic efficacy in medial prefrontal cortex. *Science*, 334(6056), 693–697.

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## Cognitive Impenetrability

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### Definition

Cognitive impenetrability is a property of the basic information processes of cognition. If a process is cognitively impenetrable, then the operation of this process cannot be altered by changing the contents of mental representations (i.e., an agent's beliefs, desires, or goals). This is because the process is "wired in" and its operation must be explained by appealing to neuroscience.

### Introduction

Six decades after experimental psychology's cognitive revolution, it is now commonplace to find studies of animal cognition. In general, the term "cognition" is synonymous to "information processing." Thus, theories of animal cognition are theories about how animals process information. However, cognitive theories also carry more technical and specific requirements. In particular, a cognitive theory distinguishes between the contents of mental representations and the information processing mechanisms that manipulate these contents. The core information processing

mechanisms of cognition are called the cognitive *architecture* (Pylyshyn 1984). Pylyshyn (p. 30) defines the cognitive architecture as "the basic operations for storing and retrieving symbols, comparing them, treating them differently as a function of how they are stored (hence, as a function of whether they represent beliefs or goals), and so on, as well as such basic resources and constraints of the system, as a limited memory."

### Wired Cognition and Cognitive Impenetrability

One of the key characteristics of the cognitive architecture is that it is presumed to be largely innate, relatively permanent, and directly implemented by neural processes. That is, the architecture defines the properties of what has been called "wired cognition" (Magnani 2009). This is a fundamentally important property, because explaining the functioning of a component of the cognitive architecture requires an account of how the brain implements this component. Thus, by ultimately grounding a cognitive theory in an architecture, one converts a cognitive description into a cognitive explanation (Dawson 2013). The architecture is the bridge between cognition and the brain. As a result, for their cognitive theories to be explanations, researchers must identify the cognitive architecture.



## The Cognitive Penetrability Criterion

How does one defend the claim that some cognitive function is part of the architecture? One methodology, the *cognitive penetrability criterion*, is inspired by the architecture's "wired-in" nature (Pylyshyn 1984, 1999). If a function is part of the architecture, then it will not be affected by changes in cognitive content – changing beliefs should not result in a changing architecture. This means that the architecture is *cognitively impenetrable*. In contrast, if changes in cognitive content produce changes in the operation of the function, then the function is *cognitively penetrable*. "If a system is cognitively penetrable then the function it computes is sensitive, in a semantically coherent way, to the organism's goals and beliefs, that is, it can be altered in a way that bears some logical relation to what the person knows" (Pylyshyn 1999, p. 343). The architecture is *not* cognitively penetrable. Finding that a function is cognitively penetrable indicates that it is *not* part of the architecture.

In studies of human cognition, the cognitive penetrability criterion is used to validate claims that particular functions belong to the architecture. In general, this involves observing the operation of the function, then changing a belief that is semantically related to the function, and finally determining whether the operation of the function changes. If it changes in a fashion that is semantically linked to the changed belief, then the function is cognitively penetrable and is not part of the architecture. This paradigm has been used to challenge the claim that certain operations on mental images, like scanning, are not part of the architecture (Pylyshyn 1984). The cognitive penetrability criterion has also been used in the study of apparent motion to show that the processes that track the identities of objects in apparent motion are likely part of the architecture because they are not affected by changes in beliefs about whether objects are moving in depth or not (Wright and Dawson 1994). However, Wright and Dawson also show the processes that create the appearance of an object in illusory motion can be penetrated by beliefs about depth of movement and therefore are not part of the architecture.

Of course, the cognitive penetrability criterion is much easier to apply in the study of human cognition than it is in the study of animal cognition. This is because it is much harder to verify than one has manipulated the beliefs of animal subjects. However, animal investigations that parallel human experiments are possible. For instance, studies that support the claim that a particular animal behavior is controlled by instinct (and not by higher-order processing) help establish that the behavior is controlled by the architecture, given the view that instincts are examples of wired cognition (Magnani 2009).

Consider one notable example from the study of nest building by wasps. Ethologist W.H. Thorpe reviewed studies of nest building in a variety of animals, including wasps, and proposed that nest construction behaviors were controlled by an *ideal releaser* (Thorpe 1963). An ideal releaser serves the role of a cognitive representation. "The bird must have some 'conception' of what the completed nest should look like, and some sort of 'conception' that the addition of a piece of moss or lichen here and here will be a step towards the 'ideal' pattern, and that other pieces there and there would detract from it" (Thorpe 1963, p. 22). With this type of theory, one would hypothesize that small damage to a physical nest, making it slightly different from the mentally represented ideal releaser, would produce behaviors that simply repair the damage to make the actual agree with the desired mental content.

However, this hypothesis is not confirmed by the behavior of the mud wasp *Paralastor* (Smith 1978). This wasp builds its nest by digging a hole in the ground, lining the hole with mud, and then building an elaborate funnel on top of the hole to keep parasites out. The funnel is a long straight tube, to which is added a marked curve; a large bell-shaped opening is attached to the end of the curve. Smith created a hole in the curve that the wasp added to the straight tube. Instead of causing the wasp to simply patch the hole as might be expected from the ideal releaser theory, this instead led the wasp to create a brand-new tube out from the hole in the curve, producing a second funnel structure built on top of the first. The



irrationality of this behavior can be taken as evidence that this wasp's nest building is cognitively impenetrable, part of the animal's architecture, and best explained by appealing to sequences of instincts governed by stigmergy (Karsai 1999).

Researchers in animal cognition have access to other methodologies for supporting claims that particular processes are part of the architecture. These too rely on the assumption that if a process is cognitively impenetrable, then it is directly implemented by the brain; it is wired cognition. Thus, any techniques that can elucidate the neural mechanisms that instantiate specific information processing can be used to argue that this processing is cognitively impenetrable and is part of the architecture.

For instance, it has long been argued that a great deal of early human visual processing is cognitively impenetrable (Pylyshyn 1999), and this hypothesis is typically supported by grounding computational or cognitive models of visual perception in the neural circuitry of early vision (Marr 1982). This evidence is largely the product of single-cell recording studies of animal brains. A variety of methods exist for studying how the brain implements many other cognitive processes, including learning, memory, and navigation (Kandel et al. 2013). It is reasonable to predict that this kind of evidence will more likely be used in the future to map the architecture of animal cognition than will be evidence collected using animal analogs of the cognitive penetrability criterion.

## Cross-References

- ▶ Cognition
- ▶ Information Processing
- ▶ Instinct
- ▶ Nest Construction
- ▶ Neural Control of Behavior
- ▶ Representation

## References

- Dawson, M. R. W. (2013). *Mind, body, world: foundations of cognitive science*. Edmonton, AB: Athabasca University Press.
- Kandel, E. R., Schwartz, J. H., Jessell, T. M., Siegelbaum, S. A., & Hudspeth, A. J. (2013). *Principles of neural science* (5th ed.). New York: McGraw-Hill.
- Karsai, I. (1999). Decentralized control of construction behavior in paper wasps: An overview of the stigmergy approach. *Artificial Life*, 5, 117–136.
- Magnani, L. (2009). *Abductive cognition: The epistemological and eco-cognitive dimensions of hypothetical reasoning*. Berlin/Heidelberg: Springer Verlag.
- Marr, D. (1982). *Vision*. San Francisco, CA: W.H. Freeman.
- Pylyshyn, Z. W. (1984). *Computation and cognition*. Cambridge, MA: MIT Press.
- Pylyshyn, Z. W. (1999). Is vision continuous with cognition? The case for cognitive impenetrability of visual perception. *Behavioral and Brain Sciences*, 22(3), 341–423.
- Smith, A. P. (1978). Investigation of mechanisms underlying nest construction in mud wasp *Paralastor* sp. (*Hymenoptera Eumenidae*). *Animal Behaviour*, 26 (Feb), 232–240.
- Thorpe, W. H. (1963). *Learning and instinct in animals* (New ed.). London: Methuen.
- Wright, R. D., & Dawson, M. R. W. (1994). To what extent do beliefs affect apparent motion? *Philosophical Psychology*, 7, 471–491.

# G

## Goggles Experiment

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The goggles experiment is the common name of an experimental procedure proposed by Cecilia Heyes (1998) with the aim of distinguishing the theory of mind hypothesis of behavior from non-mentalist alternatives. The theory of mind hypothesis claims that nonhuman animals, most notably chimpanzees and other primates, have a concept of mental states like “see,” “want,” or “know” (Premack and Woodruff 1978). Heyes’ objection was that all experiments and observations supporting this claim could also be interpreted with alternative explanations like associative learning or inferences that did not require mental state attribution.

The original goggles experiment is based on a guesser-knower paradigm (Povinelli et al. 1990), and the procedure consists of three phases:

1. In the *pre-training*, chimpanzees would be trained to wear two pairs of goggles that are only distinguishable from the outside by an arbitrary cue like different rim colors. Only by wearing the goggles, chimpanzees would experience that one pair is opaque while the

other is translucent. They would never experience anybody else wearing the goggles at this point.

2. In the *training*, chimpanzees would watch an experimenter hiding food underneath cups behind an occluder. One trainer would be present for the baiting, while a second trainer would leave the room and come back after the baiting. Both would then indicate one of the cups, and chimpanzees are rewarded for choosing the cup indicated by the trainer who saw the baiting (the knower) and never for choosing the cup indicated by the one who left the room (the guesser).
3. In *transfer*, training trials would be interspersed with probe trials in which both trainers remain in the room but wear the pairs of goggles from the pre-training. In this case, the trainer wearing the translucent goggles would be the knower and therefore the right choice if chimpanzees have a concept of seeing. Importantly, chimpanzees would not be rewarded differentially in probe trials to avoid associative learning.

Heyes argued that if chimpanzees take the knower’s cues in probe trials more often than the guesser’s, it would distinguish between the theory of mind hypothesis and non-mentalist alternatives as it can only be based on using their own mental experience to infer the others’ mental states.

Other variations of the goggles experiment have been proposed. Povinelli and Vonk (2003) suggested simplifying the procedure in a way that does not involve the extra step of distinguishing between knowing and guessing. In this version, chimpanzees can choose to beg for food between two experimenters—one wearing an opaque bucket over their head and one wearing a translucent one. If the chimpanzees preferentially gestured to the latter, it would show that they understand who can and who cannot see them.

In general, a “goggles experiment” has to follow the basic structure of (1) experiencing the properties of unknown eye covers that cannot be inferred from the outside and can only be distinguished by an arbitrary cue and (2) transferring this experience to a novel situation in which others look through these covers and make inferences about their mental states.

Recently, a study based on this general structure has been conducted with chimpanzees with positive results and has therefore been suggested to support the claim of mental state attribution in chimpanzees (Karg et al. 2015). However, the interpretation of these and other results supporting the theory of mind hypothesis in nonhuman animals, including primates and corvids, still remains a debated topic of animal cognition.

## Cross-References

- ▶ [Brian Hare](#)
- ▶ [Cecilia Heyes](#)
- ▶ [Daniel Povinelli](#)
- ▶ [Guesser-knower](#)
- ▶ [Josep Call](#)
- ▶ [Michael Tomasello](#)
- ▶ [Theory of Mind](#)

## References

- Heyes, C. M. (1998). Theory of mind in nonhuman primates. *Behavioral and Brain Sciences*, 21(01), 101–114.
- Karg, K., Schmelz, M., Call, J., & Tomasello, M. (2015). The goggles experiment: Can chimpanzees use self-experience to infer what a competitor can see? *Animal Behaviour*, 105, 211–221.
- Povinelli, D. J., & Vonk, J. (2003). Chimpanzee minds: Suspiciously human? *Trends in Cognitive Sciences*, 7(4), 157–160.
- Povinelli, D. J., Nelson, K. E., & Boysen, S. T. (1990). Inferences about guessing and knowing by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, 104(3), 203.
- Premack, D., & Woodruff, G. (1978). Does the chimpanzee have a theory of mind? *Behavioral and Brain Sciences*, 1(04), 515–526.

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## Ronald Weisman

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Ronald G. Weisman made major contributions to the field of Comparative Cognition for over 50 years. Ron finished his career as Professor Emeritus in the Departments of Psychology and Biology at Queen's University located in Kingston, Ontario. Ron was born in Detroit, Michigan, in 1937 and died in Kingston, Ontario, in 2015. Ron earned a B.A. (1960), M.A. (1961), and Ph.D. (1964) from Michigan State University. Ron's first research publications came from work that employed principles of learning in an educational setting (e.g., Krumboltz and Weisman 1962). Ultimately, Ron completed his graduate work with Jack King and M. Ray Denny studying animal behavior with a focus on learning processes in

mice (e.g., Denny and Weisman 1964; King and Weisman 1964).

Following his graduate work at MSU, Ron was a National Science Foundation (NSF) postdoctoral fellow with David Premack at the University of California, Santa Barbara from 1965 to 1966. Ron was hired as Assistant Professor of Psychology at Queen's University in 1964. He was promoted to Associate Professor in 1970, again to Professor in 1977, cross appointed to the Department of Biology in 1993, and finally promoted to Professor Emeritus in 2000. In sum, Ron was a professor at Queen's for over 50 years. During his time at Queen's, Ron took up many visiting appointments at other universities, including at Duke University, Florida Tech, Johns Hopkins University, Sussex University, King's College at Cambridge University, and the University of California, San Diego.

Ron made numerous significant contributions to our understanding of animal learning, cognition, and behavior. In his early career as an independent scientist, much of his work focused on investigating the determinants of behavior, using what can be considered a traditional approach to understanding behavior: experiments conducted in conditioning chambers, using rats and pigeons as subjects (e.g., Weisman 1975). In these studies he made many contributions to understanding basic learning processes such as discrimination, inhibition, and avoidance learning. This work, although important and well regarded, is not what most people will remember as Ron's main

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Ronald G. Weisman. Ph.D., Professor Emeritus of Psychology and Biology (14 September 1937–27 January 2015)

scientific contributions. The work from the “second act” of his career is the work for which Ron will be most remembered.

In the 1980s, Ron embarked on a new career, studying all aspects of songbird vocal perception and production. Being a newcomer to the empirical study of songbirds, Ron started almost from scratch. The genesis of this new career was characterized by a series of happy coincidences, a real life evolution of a research program, if you will. Around the time of his trip to San Diego, Ron had become interested in understanding how animals process information and wanted to apply *information integration theory* as a conceptual framework to do so. Up to this point, Ron had tested his ideas with pigeons as subjects but felt that studying a natural system was a better way to proceed. It was around this same time that he met Laurene Ratcliffe, who had recently started working at Queen’s University, and asked her, as an expert in songbird behavioral ecology who had experience working with great tits (*Parus major*) at Oxford University, whether birdsong would be a good system to approach these questions. Ratcliffe suggested black-capped chickadees (*Poecile atricapillus*) as a potential model system because they had a two-note song that seemed relatively simple acoustically. One of the first set of studies involved conducting operant-type procedures in the field and the laboratory that showed chickadees were sensitive to the number, note type, and order of the notes in their song (Ratcliffe and Weisman 1986; Weisman and Ratcliffe 1987; Ratcliffe and Weisman 1988). Thus the simple song seemed to be not so simple upon closer experimentation. The happy coincidences continued when Stuart Hulse and Jeffery Cynx, who were already studying pitch perception in starlings (*Sturnus vulgaris*; Hulse and Cynx 1986), performed calculations on black-capped chickadee songs that Ratcliffe and Weisman reported in their 1985 Condor paper and pointed out to Ron and Laurene that chickadees produced their two-note songs with a consistent relative pitch relationship between the two notes. Once again, the “simple” song turned out to be paradoxical in its complexity embedded in seeming simplicity.

Ron forged a truly integrative research program that combined elements of learning, cognition, ethology, and neuroscience using a variety of songbird species as his study subjects (for reviews of some of this work, see Weisman and Ratcliffe 2004 and Weisman et al. 2012). Following the early success of this work with songbird perception, Ron also began to compare the auditory perceptual abilities of songbirds with those of humans. Ron and his colleagues (notably Laurene M. Ratcliffe, T. Andrew Hurly, Daniel M. Weary, Scott A. MacDougall-Shackleton, Douglas J.K. Mewhort, Leslie S. Phillmore, Milan G. Njegovan, Marisa Hoeschele, Laurie L. Bloomfield, and Christopher B. Sturdy) uncovered aspects of songbird production and perception that were largely unknown before Ron embarked on this new research area. Among the most notable of his research findings, Ron and his colleagues described black-capped chickadee singing behavior in detail and, among other findings, showed that chickadees produce the frequency interval in their two-note *fee-bee* song with remarkable fidelity (Horn et al. 1992; Ratcliffe and Weisman 1985; Weisman et al. 1990). Moreover, Ron showed that birds could perceive this interval with a high degree of accuracy (Weisman and Ratcliffe 1989; Weary and Weisman 1991). Importantly, Ron showed that this perceptual ability and other auditory perceptual abilities and neurobiological correlates (Njegovan and Weisman 1997, Phillmore et al. 2003) were impacted if the birds were reared in conditions that resulted in abnormal vocal production. Further studies, both with chickadees and zebra finches (*Taeniopygia guttata*), revealed that songbirds far outperformed humans, even trained musicians, at frequency-based discrimination tasks (e.g., Weisman et al. 1998; for a review see Weisman et al. 2012). Later work showed that zebra finches, like chickadees, had perceptual and production deficits following manipulations of the social, acoustic environment during development (Sturdy et al. 2001). A constant theme throughout his career was the encouragement and support he provided his collaborators and trainees, imploring them and others to conduct research aimed at “explaining nature” (Weisman 2008).

Ron's career was impressive by any measure, but his impact extends beyond that accounted by metrics like number of publications, H indices, and other such measures often used for assessment. Some of the most lasting contributions that Ron made to the scientific communities to which he was utterly devoted throughout his career defy such routine enumeration. After his death in 2015, many colleagues offered descriptions of Ron's influence using phrases such as "force of nature," "intellectually challenging," "passionate," and "inspiring." All of these things he surely was. Among Ron's many important contributions to the scientific community was his creation of an international conference designed to bring together researchers from Psychology and Biology to share their findings and insights about behavior, learning, and cognition across species. This conference, called the Conference on Comparative Cognition (CO3), started in 1994 with an attendance of approximately three dozen scientists and rapidly grew into a popular annual conference with a stable attendance at well over 100 presenters from all over the world. Over the years, there have been talks about numerous aspects of behavior and cognition on over 100 species.

In response to the growth and overwhelming success of the CO3 conference, and the recognition that a more formal organizational structure was needed, Ron founded the Comparative Cognition Society (CCS) in 1997 and was the first president of CCS. This society has grown and thrived since its founding, and Ron was awarded the CCS Research Award for his substantial contributions to the field in 2007. Ron also initiated and was the first editor and publisher of the online and open-access journal, *Comparative Cognition & Behavior Reviews*, which has published important reviews and critical commentaries on a wide range of topics in Comparative Cognition since 2006.

## Cross-References

- ▶ [Auditory Signals](#)
- ▶ [B.F. Skinner](#)

- ▶ [Charles Darwin](#)
- ▶ [Communication](#)
- ▶ [Comparative Cognition](#)
- ▶ [Comparative Psychology](#)
- ▶ [Countersinging](#)
- ▶ [Discrimination Learning](#)
- ▶ [Natural Categories](#)
- ▶ [Passerine Cognition](#)
- ▶ [Passerine Communication](#)
- ▶ [Passerine Sensory Systems](#)
- ▶ [Perception](#)

## References

- Denny, M. R., & Weisman, R. G. (1964). Avoidance behavior as a function of length of nonshock confinement. *Journal of Comparative and Physiological Psychology*, *58*, 252–257.
- Horn, A. G., Leonard, M., Ratcliffe, L. M., Weisman, R. G., & Shackleton, S. (1992). Frequency variation in the songs of black-capped chickadees. *Auk*, *109*, 847–852.
- Hulse, S. H., & Cynx, J. (1986). Interval and contour in serial pitch perception by a passerine bird, the European starling (*Sturnus vulgaris*). *Journal of Comparative Psychology*, *3*, 215–228.
- King, J. A., & Weisman, R. G. (1964). Sand digging contingent upon bar pressing in deer mice. *Animal Behavior*, *12*, 446–450.
- Krumboltz, J. D., & Weisman, R. G. (1962). The effect of overt versus covert responding to programmed instruction of immediate and delayed retention. *Journal of Educational Research*, *53*, 89–92.
- Njegovan, M., & Weisman, R. (1997). Pitch discrimination in field and isolation reared black-capped chickadees (*Parus atricapillus*). *Journal of Comparative Psychology*, *111*, 294–301.
- Phillmore, L. S., Bloomfield, L. L., & Weisman, R. G. (2003). Effects of songs and calls on ZENK expression in the auditory telencephalon of field- and isolate-reared black-capped chickadees. *Behavioural Brain Research*, *147*, 125–134.
- Ratcliffe, L., & Weisman, R. G. (1985). Frequency shift in the fee bee song of the black-capped chickadee. *The Condor*, *87*, 555–557.
- Ratcliffe, L., & Weisman, R. G. (1986). Song sequence discrimination in the black-capped chickadee (*Parus atricapillus*). *Journal of Comparative Psychology*, *100*, 361–367.
- Ratcliffe, L., & Weisman, R. (1988). Representation of conspecific song by chickadees: Comparisons among embedded 'fee bees'. *Behavioural Processes*, *17*, 199–203.
- Sturdy, C. B., Phillmore, L. S., Sartor, J. J., & Weisman, R. G. (2001). Reduced social contact causes auditory



- perceptual deficits in zebra finches, *Taeniopygia guttata*. *Animal Behaviour*, *62*, 1207–1218.
- Weary, D. M., & Weisman, R. G. (1991). Operant discrimination of frequency and frequency ratio in the black-capped chickadee (*Parus atricapillus*). *Journal of Comparative Psychology*, *105*, 253–259.
- Weisman, R. G. (1975). Stimulus control by response-dependent shock in discriminated punishment. *Bulletin of the Psychonomic Society*, *5*, 427–428.
- Weisman, R. G. (2008). Advice to young behavioral and cognitive scientists. *Behavioural Processes*, *77*, 142–148.
- Weisman, R., & Ratcliffe, L. (1987). How birds identify species information in song: A pattern recognition approach. *Learning and Motivation*, *18*, 80–98.
- Weisman, R. G., & Ratcliffe, L. (1989). Absolute and relative pitch processing in black-capped chickadees, *Parus atricapillus*. *Animal Behaviour*, *38*, 685–692.
- Weisman, R. G., & Ratcliffe, L. M. (2004). Relative pitch and the song of black-capped chickadees. *American Scientist*, *92*, 534–539.
- Weisman, R., Ratcliffe, L., Johnsrude, I., & Hurly, T. A. (1990). Absolute and relative pitch production in the song of the black-capped chickadee (*Parus atricapillus*). *Condor*, *92*, 118–124.
- Weisman, R., Njegovan, M., Sturdy, C., Phillmore, L., Coyle, J., & Mewhort, D. (1998). Frequency range discriminations: Special and general abilities in zebra finches (*Taeniopygia guttata*) and humans (*Homo sapiens*). *Journal of Comparative Psychology*, *112*, 244–258.
- Weisman, R. G., Mewhort, D. J. K., Hoeschele, M., & Sturdy, C. B. (2012). New perspectives on absolute pitch in birds and mammals. In E. A. Wasserman & T. R. Zentall (Eds.), *Handbook of comparative cognition* (pp. 67–79). New York: Oxford University Press.

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## William Roberts

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Dr. William (“Bill”) A. Roberts is an internationally renowned experimental psychologist and Emeritus Professor at Western University (London, Ontario, Canada). Born in Safford, Arizona (USA), Bill completed his Bachelor of Science at the University of Maryland in 1960 and his Masters of Arts in 1962 and Ph.D. in 1965 at Bryn Mawr College, Pennsylvania, under the supervision of Dr. M.E. Bitterman. Bill was briefly a faculty member at Vassar College, New York, before moving to Canada, first as a postdoc with Dr. Endel Tulving at the University of Toronto from 1968 to 1969 and then as a faculty member at Western starting in 1970.

Dr. Roberts has authored over 160 publications, including well-regarded books such as *Processes of Animal Memory* (Medin et al. 2014) and *Principles of Animal Cognition* (Roberts 1998) and highly cited articles such as “Are animals stuck in time?” (Roberts 2002). Dr. Roberts has studied a wide variety of cognitive processes in animals, including metacognition, time and number representation, memory, future anticipation, and transitive inference. His study subjects have been likewise varied and have included humans, rats,

pigeons, dogs, horses, and squirrel monkeys. Dr. Roberts’ early work was pioneering in the field of animal memory processes, especially in the use of delayed matching-to-sample to study working memory (e.g., Roberts 1972; Roberts and Grant 1974, 1976, 1978). Some of his best-known recent work includes the comparison of time and number representations in pigeons (e.g., Roberts 2006; Roberts and Boisvert 1998; Roberts et al. 1989, 2000; Roberts and Mitchell 1994), mental time travel in monkeys, chickadees, and rats (e.g., McKenzie et al. 2004; Naqshbandi and Roberts 2006; Roberts 2007, 2016; Roberts et al. 2008; Roberts and Feeney 2009), and the competition between working and reference memory processes (Roberts et al. 2015, 2016).

Dr. Roberts has held uninterrupted grant funding from the Natural Sciences and Engineering Research Council of Canada (or, previously, the National Research Council Canada) since 1969. Since his retirement in 2004, Dr. Roberts has maintained a highly active lab, with many publications in top-tier journals in animal cognition as well as publications in high-impact journals such as *Trends in Cognitive Sciences*, *Current Biology*, and *Science*. He has been Editor for the journal *Learning & Motivation* since 2000. His research has also been highlighted in a number of newspaper and other popular media, including a large segment in a 2015 episode of *The Nature of Things*, *A Dog’s Life*. He has previously been Chair of the Department of Psychology at Western University and is a Fellow of

Divisions 3 and 6 of the American Psychological Association. Dr. Roberts was also honored with the Comparative Cognition Research Award in 2005 from the Comparative Cognition Society (of which he is a founding member) for his lifetime of achievement in the field.

## References

- McKenzie, T., Cherman, T., Bird, L. R., Naqshbandi, M., & Roberts, W. A. (2004). Can squirrel monkeys (*Saimiri sciureus*) plan for the future? Studies of temporal myopia in food choice. *Learning & Behavior, 32*, 377–390.
- Naqshbandi, M., & Roberts, W. A. (2006). Anticipation of future events in squirrel monkeys (*Saimiri sciureus*) and rats (*Rattus norvegicus*): Tests of the Bischof-Kohler hypothesis. *Journal of Comparative Psychology, 120*, 345–357.
- Roberts, W. A. (1972). Short-term memory in the pigeon: Effects of repetition and spacing. *Journal of Experimental Psychology, 94*, 74–83.
- Roberts, W. A. (2002). Are animals stuck in time? *Psychological Bulletin, 128*, 473–489.
- Roberts, W. A. (2006). Evidence that pigeons represent both time and number on a logarithmic scale. *Behavioural Processes, 72*, 207–214.
- Roberts, W. A. (2007). Mental time travel: Animals anticipate the future. *Current Biology, 17*, R418–R420.
- Roberts, W. A. (2016). Episodic memory: Rats master multiple memories. *Current Biology, 26*, R920–R922.
- Roberts, W. A., & Boisvert, M. (1998). Using the peak procedure to measure timing and counting processes in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes, 24*, 416–430.
- Roberts, W. A., & Feeney, M. C. (2009). The comparative study of mental time travel. *Trends in Cognitive Sciences, 13*, 271–277.
- Roberts, W. A., & Grant, D. S. (1974). Short-term memory in the pigeon with presentation precisely controlled. *Learning and Motivation, 5*, 393–408.
- Roberts, W. A., & Grant, D. S. (1976). Studies of short-term memory in the pigeon using the delayed matching-to-sample procedure. In D. L. Medin, W. A. Roberts, & R. T. Davis (Eds.), *Processes of animal memory*. Hillsdale, NJ: Erlbaum.
- Roberts, W. A., & Grant, D. S. (1978). Interaction of sample and comparison stimuli in delayed matching to sample with the pigeon. *Journal of Experimental Psychology: Animal Behavior Processes, 4*, 68–82.
- Roberts, W. A., & Mitchell, S. (1994). Can a pigeon simultaneously process temporal and numerical information? *Journal of Experimental Psychology: Animal Behavior Processes, 20*, 66–78.
- Roberts, W. A., Cheng, K., & Cohen, J. S. (1989). Timing light and tone signals in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes, 15*, 23–35.
- Roberts, W. A., Coughlin, R., & Roberts, S. (2000). Pigeons flexibly time or count on cue. *Psychological Science, 11*, 218–222.
- Roberts, W. A., Feeney, M. C., MacPherson, K., Petter, M., McMillan, N., & Musolino, E. (2008). Episodic-like memory in rats: Is it based on when or how long ago? *Science, 320*, 113–115.
- Roberts, W. A., Strang, C., & Macpherson, K. (2015). Memory systems interaction in the pigeon: Working and reference memory. *Journal of Experimental Psychology: Animal Learning and Cognition, 41*, 152.
- Roberts, W. A., Macpherson, K., & Strang, C. (2016). Context controls access to working and reference memory in the pigeon (*Columba livia*). *Journal of the Experimental Analysis of Behavior, 105*, 184–193.