

# C

## Catarrhine Sensory Systems

Julie A. Teichroeb and L. Tamara Kumpan  
University of Toronto,  
Toronto, ON, Canada

### Definition

The Catarrhini are an Infraorder of the Order Primates that includes the Old World monkeys, apes, and humans. Sensory systems are the ways in which animals perceive and experience the world around them.

### Introduction

All living things have evolved sensory modalities to take in information about their environment, allowing them to react in appropriate ways to best enhance their survival and reproduction. In mammals, these modalities are often discussed as the five senses (i.e., sight, hearing, smell, taste, and touch). However, the mammalian sensory system also includes rarely considered senses, such as proprioception and other senses internal to the body. Below, we discuss each of these modalities and how catarrhines use them.

## The Five Senses

### Vision

Primates rely primarily on visual information for many important daily activities, including evaluating predation threats, navigating interactions with conspecifics, and during foraging bouts. Among the primates, some have developed a specialized ability for color vision (trichromacy) which is unique in comparison to other eutherian mammals, who are thought to be either dichromatic or monochromatic. However, not all primates are consistently trichromatic; routine color vision evolved only in the catarrhines and in one other taxa (New World howler monkeys). All catarrhine species are considered routine trichromats, where both males and females are capable of color vision (Lucas et al. 2003). More specifically, this means that all catarrhines have the ability to distinguish between lights of different spectral composition regardless of brightness, and further, between red and green coloration (SurrIDGE et al. 2003). This is in contrast to most platyrrhines (New World monkeys excluding howlers) and all strepsirrhines (lemurs and lorises), where trichromacy is generally a polymorphic trait and only females are capable of trichromacy.

Physiologically, trichromacy in primates is achieved through the actions of photoreceptor cells, called cone cells, in the retina of the eye. These cone cells generate responses that are then compared with each other by neural mechanisms to generate color signals. Some of this processing

of color cues is thought to occur in the primary visual cortex (V1), but it is not yet clear to what extent. Cone cells house photopigments; in primates, the primary photopigment is opsin. Importantly, these cone cells differ in their spectral sensitivity, or more simply, the wavelengths of light they are sensitive to. Most mammals possess only two kinds of cone receptors, one of which responds to short-wavelength light of about 430 nm and is conventionally known as the S cone and another that responds to long-wavelength light of about 560 nm and is conventionally known as the L cone. The combination of only two cones renders most nonprimate mammals dichromatic. However, in catarrhines, trichromacy is possible due to an additional cone receptor in the eyes that is maximally sensitive to middle-wavelength light of about 530 nm, which is conventionally known as the M cone. This additional cone arose early in the catarrhine lineage through a duplication in the gene for the long-wavelength cone that caused it to diversify into two kinds of cones with differences in peak sensitivities. More specifically, routinely dichromat primates possess a single gene coding for L cone pigments and M cone pigments, which is located on the X chromosome. However, in catarrhines, this gene was duplicated resulting in separate L and M cone pigments with differing spectral sensitivities. The signals produced by this additional M cone are then compared by a second neural subsystem: the relatively more modern “red-green” mechanism compares L with M cone signals, while an evolutionarily older “blue-yellow” mechanism compares S cone signals with both L and M cone signals combined. Because most platyrrhine primates do not have this duplicated M/L gene, males are thus genetically restricted to receiving only either an M or L opsin pigment on their X chromosome in addition to an S opsin (which is encoded by an autosomal gene). This limits them to dichromacy. Thus, among platyrrhine primates other than howlers, only heterozygous females can express trichromacy, but both male and female catarrhine primates are trichromatic.

In catarrhines, trichromacy is thought to have evolved to aid in foraging, either in the selection

of ripe fruits or young leaves. This is because younger and more preferred leaves tend to be redder in color than more mature (and thus less preferred) leaves, which become green at mature stages of growth. The additional M cone enables all catarrhines to see young leaves among mature foliage, as the phylogenetically newer L/M subsystem allows for the detection of brighter, more colorful targets amidst a contrasting green background. In addition, ripe fruits shift to a variety of colors during maturation, causing them to stand out as well among unripe fruits and leaves. Therefore, for catarrhines foraging for either young leaves or ripe fruits, consistent color signals are thought to be a more reliable strategy in finding food than other cues such as lighting or form. This is simply because lighting and form cues can be much more variable and thus less reliable than color cues. Further, the evolution of full trichromatic vision appears to coincide with a deterioration of the sense of smell, suggesting an increased reliance on such visual coloration cues. It has also been proposed that trichromacy can be useful in detecting intraspecific signals (Allen 1879). For example, ovulating females of some species display distinctive red sexual swells, males may signal high testosterone with red skin ornaments, and many colobine infants have bright neonatal coats in orange hues.

Another primate visual adaptation is the evolution of orbital convergence. Forward-facing eyes allow for binocular vision leading to excellent depth perception. This is important because early primates spent much of their time in trees. Binocular vision could therefore have allowed tree-dwelling primates to accurately judge distances when jumping between trees and branches. Additionally, the presence of a fovea centralis amplifies the effect of increased depth perception in haplorrhines as well as that of trichromacy in the catarrhines. The fovea centralis is a tiny pit located in the central retina that enables these primates to see sharp details and color and to have excellent central vision. In the fovea, light is able to fall directly onto the cones to produce maximum visual acuity. The fovea is thought to have evolved in stem haplorrhines and is a visual

feature characteristic of both catarrhine and platyrrhine primates (Williams et al. 2010).

### Audition

In general, primate vocalizations serve to convey information about internal motivational states and the surrounding environment, including conspecifics and inanimate objects (Hauser 1993). These vocalizations are produced through movements of the lungs, larynx, and the supralaryngeal vocal tract (Ghazanfar 2010). Hearing is known to be a multimodal sensory ability in primates, in that the auditory cortex integrates information from multiple sensory avenues. This includes the integration of visual information, such as when one links visual and auditory communication signals (e.g., matching facial expressions to congruent vocal expressions). The speed and accuracy of the visual orienting reflex is also an example of the integration of auditory and visual areas in the brain. Interestingly, auditory areas also appear to integrate tactile information, for example integrating the kinesthetic feedback from one's own speech movements with heard speech. In early primates, increased visual field overlap may have been associated with selection for increased sound localization abilities (Dominy et al. 2004). This is because in other animals, increased visual acuity positively correlates with a well-developed ability to localize a sound in space. More specifically, in other mammals sound localization abilities correlate with the width of the field of best vision, in that species with narrow fields of best vision (i.e., a fovea) have better abilities to localize sound than mammals with broad fields of best vision (Heffner 2004). Importantly, this trend holds for primates; the two species for which visual acuity and field of best vision are both known are relatively good sound localizers. As others have proposed, it may be that good sound localization acuity was evolutionary selected for its usefulness in directing vision (Heffner 2004). Primates are also similar to other mammals in that smaller species are capable of hearing relatively higher frequencies than larger species, but all primates appear to have relatively good low-frequency hearing; humans in particular have highly restricted high-frequency hearing.

Regarding the auditory sense, there are distinctive anatomical features that separate the catarrhine auditory sense from that of other primates. For example, all catarrhines have evolved a complete bony canal that leads from the ear drum to the external auditory meatus (outer ear hole) and is visible on the outside of the skull. This bony canal is called the ectotympanic tube. The ectotympanic tube is formed by the ectotympanic bone, which consists of both a bony part and an external cartilaginous part. Put simply, this tube connects the tympanic membrane to the external ear. Tarsiers have also evolved a bony ectotympanic tube, but New World monkeys and prosimians have not (though in many species, a tube made up of cartilage is present). In regards to function, the ectotympanic tube has been proposed to be an adaptation to reduce the amount of noise produced during mastication (Fricano and DeLeon 2016).

The ability to produce and comprehend speech is perhaps the most unique catarrhine capability but is restricted to only one extant species: humans. Physiologically, nonhuman primates are constrained in their ability to produce language by their anatomy and neural mechanisms. However, the neural mechanisms available in nonhuman primate brains are likely to have contributed to the evolution of human speech, in that human language appears to have built on mechanisms and structures available in nonhuman primate brains. Language processing is multimodal and is carried out in part by several different regions of the brain, including the well-identified Broca's and Wernicke's areas. These areas are well known to be crucial in the production of language (Broca's area) and in the comprehension of language (Wernicke's area). The only nonhuman primates thought to have a well-developed frontal lobe containing a functional homologue to one of these areas are catarrhines. In catarrhine primates, the anatomical and functional homologue to Broca's area is thought to be located in a section of the monkey premotor cortex (Fogassi and Ferrari 2007). Interestingly, this area houses audiovisual mirror neurons that discharge when a monkey performs an action and hears the corresponding sound (e.g., tearing paper and

hearing a rip). This area and related structures may have evolved to exercise control over orofacial actions related to communication, but in humans may have come to control actions related to speech as well. Thus, the production and comprehension of language is a complex ability limited to humans but has clear roots in the anatomy and neural structures that currently exist in nonhuman primates.

### Olfaction

Relative to other mammals and other primates, the catarrhine sense of smell is reduced. Mammals usually have two systems to take in scent information from airborne molecules, the main olfactory system, which detects volatile odorants, and the accessory olfactory system, primarily made up by the vomeronasal organ (VNO), which detects nonvolatile odorants of heavier molecular weights (e.g., pheromones) (Dominy et al. 2004). However, catarrhines have lost the use of the VNO and the olfactory bulb that processes scent information is small relative to other primates. It has been hypothesized that the importance of trichromatic color vision in catarrhines may have relaxed the need for sensitive smell. Old World monkeys, apes, and especially humans have all lost the functioning of many of their olfactory receptor genes, which have been replaced by pseudogenes. Trichromatic New World howler monkeys show a similar pattern but this high rate of loss in functional olfactory receptor genes is not seen in dichromatic species or those polymorphic for color vision (Gilad et al. 2004). The timing of loss of the VNO in the catarrhine lineage also corresponds roughly with the evolution of trichromacy 25–40 million years ago. Catarrhines are notable for the degree to which color is used as signals of dominance and fertility, so it is possible that visual information that was available with routine trichromacy made information on pheromones gathered from the VNO redundant (Liman 2006). Even without a VNO, catarrhines are still known to detect some phenomenal cues but appear to do this with the main olfactory system.

### Gustation

It is appropriate to discuss taste immediately after smell, since the two are intricately linked when animals are selecting and experiencing resources. Gustation actually occurs when the stereochemical structure of a substance being tasted is recognized by taste bud sensory cells on the tongue, causing gustatory nerve fibers to fire, transmitting impulses to the brain of different taste sensations. However, what people normally think of as the “taste” of something is actually the interaction of a suite of sensory perceptions, including most strongly the odor and reaction of taste receptors, but also the feeling of it touching the tongue, any irritation to the mouth caused by compounds within it, and perception of the temperature (Hladik and Simmen 1996). Prior to more intensive research, it was thought that primates could recognize four basic tastes, including salt, sweet, bitter, and sour. The taste of umami, which includes glutamic acid and its derivatives was added to this list later (Kawamura and Kare 1987). The notion of basic tastes is still often used but research on taste physiology has shown that most of the taste bud sensory cells located on the tongue will react to several substances though they may have higher affinities for certain ones (Faurion 1987). This suggests that taste sensations are more of a continuum rather than a set of basic tastes. Research on several primate species has shown that tasting abilities cluster in closely related taxa and differ when species are less related. In accordance with this, human and chimpanzee tasting abilities are very similar but some minor differences have been found between apes and Old World monkeys (Hellekant et al. 1997).

Taste perceptions, preferences and aversions have clear evolutionary importance. For instance, bitter, sour, and astringent substances elicit a strong taste aversion in primates and many of these (e.g., alkaloids, tannins, saponins, terpenes) are toxic. The three other “basic tastes,” sweet, salty, and umami often indicate nutritive content (Liman 2006). Primates show a correlation between body size and the threshold in the ability to detect sucrose and fructose, important sugars

found in fruit. Larger primates have lower thresholds and thus a greater ability to detect minute concentrations of sugars. This may be due to larger animals having a greater area of lingual mucosa on the tongue leading to better taste acuity. This ability likely allows these larger primates to find a wide array of food stuffs palatable, helping them maintain their body size (Hladik and Simmen 1996).

### **Somatosensation**

The sense of touch can be defined as somatosensory perception that allows an organism to take in information on pressure, vibrations, itches, pain, and temperature. Sometimes included in somatosensation are also the muscular and visceral sensations that can be perceived from inside the body (interoception). Primates appear to have a strong awareness of their internal homeostatic afferent activity and if the physiological condition of any part of the body is not normal this will be perceived by autonomic motor control and communicated to the brain with sensations such as thirst, hunger, discomfort, or pain (Craig 2003).

Different types of cutaneous receptors take in various forms of tactile information. Touch is perceived with rapidly adapting cutaneous mechanoreceptors like Meissner corpuscles, hair follicle receptors, and free nerve endings. Pressure is more likely to be detected with slow adapting cutaneous mechanoreceptors like Merkel corpuscles. Temperature is perceived with thermoreceptors and pain and itch are perceived by nociceptors (Mada 2000). The anthropoid primates, a classification that includes all catarrhines, are particularly notable for the density of cutaneous mechanoreceptors on the hand (Dominy et al. 2004). The hand is the most important sensory organ for tactile stimulus in catarrhines and almost all species have fine motor control, long fingers, an opposable or semiopposable thumb, and nails instead of claws, allowing the sensitive finger tips to be exposed. Mechanoreceptors for touch are especially located on the glabrous skin of the palm and palmar aspect of the fingers, where

different types of sensory endings are found in the thick epidermal layer that forms patterns of ridges and grooves (Vallbo and Johansson 1984). Parts of the brain in the thalamus and cortex are primarily responsible for taking in somatosensory information.

Touch plays an extremely important role in communication in catarrhines, allowing information transfer through tactile means. Different types of touch are ascribed meaning but this may be changed or tempered depending on the situation and the duration or intensity of the touch (Hertenstein et al. 2006). For instance, a kick may be aggressive but if it is done lightly in a playful situation the meaning can be changed completely. The most developed sensory modality for infant catarrhines at birth is touch and it has been shown to regulate infant psychological states and aid in normal biological and social development. In humans, physical contact between mothers and infants is key in bond formation, with more frequent and nurturing contact from the mother leading to more secure children later. As the other senses become keener into adulthood, touch does not have the over-riding importance that it has for infants; however, it is still vital for people in many interactions, in particular compliance, power relations, intimacy, and hedonic perception (Hertenstein et al. 2006).

One of the main tactile behaviors seen in catarrhines (in both nonhumans and humans) is grooming. While grooming does have a hygienic function, it is also very important in bonding and status maintenance. In Old World monkeys and apes, individuals generally spend more time grooming those that are kin or closer to them in dominance rank and grooming tends to go up the hierarchy with more dominant individuals receiving more than subordinates (Schino 2001). Grooming has also been shown to relieve stress, aid in reconciliation following aggression, and build bonds that may later lead two individuals to support one another in aggressive encounters (Dunbar 2010).

## The Neglected Sense

### Proprioception

In order for animals to control their movements, they must be aware of where their body is in space. Three systems are primarily used to do this, the felt position of the body (proprioception or the kinesthetic sense), visual cues regarding where the body (and each limb) is located, and tactile cues of body parts touching substrates. All of this information is processed in the premotor cortex in catarrhines. In particular, proprioception has been discussed in four broad sets of sensory perceptions: the sense of position and movement, the sense of tension, the sense of effort or heaviness, and the sense of balance (equilibrioception). Different but related mechanisms appear to be used for these four sets of perceptions (Gandevia 1996). Tendon organs allow a sense of tension and the central nervous system is responsible for the sense of effort. Sensing of position and movement is done through muscle spindles and receptors in skin and joints but also through the vestibular system, which additionally provides the sense of balance. The vestibular system in the inner ear contains three semicircular canals that sense rotational movement and two otolith organs, called the utricle and saccule, that sense acceleration. Research has shown that the vestibular system has extensive convergence with many other sensory systems, acquiring constant signals from the eyes, muscles, joints, and skin, making it extremely important in everyday function for animals (Angelaki and Cullen 2008).

### Conclusion

Compared to primates that retain more primitive ancestral characteristics, catarrhine sensory systems are most notable for routine trichromatic color vision, a reduction in the olfactory sense, and the importance of the hand as a sensory organ.

### Cross-References

► [Platyrrhine Sensory Systems](#)

- [Primate Sensory Systems](#)
- [Prosimian Sensory Systems](#)
- [Sensory Adaptation](#)
- [Sensory Receptors](#)

### References

- Allen, G. (1879). *The colour-sense: Its origin and development; an essay in comparative psychology*. London: Paul, Trench, Trübner.
- Angelaki, D. E., & Cullen, K. E. (2008). Vestibular system: The many facets of a multimodal sense. *Annual Review of Neuroscience*, *31*, 125–150.
- Craig, A. D. (2003). Interoception: The sense of the physiological condition of the body. *Current Opinion in Neurobiology*, *13*, 500–505.
- Dominy, N. J., Ross, C. F., & Smith, T. D. (2004). Evolution of the special senses in primates: Past, present, and future. *The Anatomical Record Part A: Discoveries in Molecular, Cellular, and Evolutionary Biology*, *281*, 1078–1082.
- Dunbar, R. I. M. (2010). The social role of touch in humans and primates: Behavioural function and neurobiological mechanisms. *Neuroscience and Biobehavioral Reviews*, *34*, 260–268.
- Faurion, A. (1987). Physiology of the sweet taste. In D. Otosson (Ed.), *Progress in sensory physiology* (pp. 130–201). Heidelberg: Springer-Verlag.
- Fogassi, L., & Ferrari, P. F. (2007). Mirror neurons and the evolution of embodied language. *Current Directions in Psychological Science*, *16*, 136–141.
- Fricano, E. E., & DeLeon, V. B. (2016). Scaling of the ectotympanic tube and tympanic membrane diameter among catarrhine primates. *The FASEB Journal*, *30* (1 Suppl), 779.
- Gandevia, S. C. (1996). Kinaesthesia: Roles for afferent signals and motor commands. In L. B. Rowell & J. T. Shepherd (Eds.), *Handbook of physiology* (pp. 128–172). New York: Oxford University Press.
- Ghazanfar, A. A. (2010). The default mode of primate vocal communication and its neural correlates. In *Multisensory object perception in the primate brain* (pp. 139–153). New York: Springer.
- Gilad, Y., Wiebe, V., Przeworski, M., Lancet, D., & Pääbo, S. (2004). Loss of olfactory receptor genes coincides with the acquisition of full trichromatic vision in primates. *PLoS Biology*, *2*, 0120.
- Hauser, M. D. (1993). The evolution of nonhuman primate vocalizations: Effects of phylogeny, body weight, and social context. *The American Naturalist*, *142*, 528–542.
- Heffner, R. S. (2004). Primate hearing from a mammalian perspective. *The Anatomical Record Part A: Discoveries in Molecular, Cellular, and Evolutionary Biology*, *281*, 1111–1122.
- Hellekant, G., Danilova, V., & Ninomiya, Y. (1997). Primate sense of taste: Behavioral and single chorda tympani and glossopharyngeal nerve fiber recordings in the

- Rhesus monkey, *Macacaulatta*. *Journal of Neurophysiology*, 77, 978–993.
- Hertenstein, M. J., Verkamp, J. M., Kerestes, A. M., & Holmes, R. M. (2006). The communicative functions of touch in humans, nonhuman primates, and rats: A review and synthesis of the empirical research. *Genetic, Social, and General Psychology Monographs*, 132, 5–94.
- Hladik, C. M., & Simmen, B. (1996). Taste perception and feeding behavior in nonhuman primates and human populations. *Evolutionary Anthropology*, 5, 58–71.
- Kawamura, Y., & Kare, M. R. (Eds.). (1987). *Umami: A basic taste*. New York: Marcel Dekker.
- Liman, E. R. (2006). Use it or lose it: Molecular evolution of sensory signaling in primates. *Pflügers Archiv*, 453, 125–131.
- Lucas, P. W., Dominy, N. J., Riba-Hernandez, P., Stoner, K. E., Yamashita, N., Loría-Calderón, E., Petersen-Pereira, W., Rojas-Durán, Y., Salas-Pena, R., Solís-Madrigal, S., & Osorio, D. (2003). Evolution and function of routine trichromatic vision in primates. *Evolution*, 57, 2636–2643.
- Mada, S. S. (2000). *Human biology*. New York: McGraw Hill.
- Schino, G. (2001). Grooming, competition and social rank among female primates: A meta-analysis. *Animal Behaviour*, 62, 265–271.
- Surridge, A. K., Osorio, D., & Mundy, N. I. (2003). Evolution and selection of trichromatic vision in primates. *Trends in Ecology & Evolution*, 18, 198–205.
- Vallbo, A. B., & Johansson, R. S. (1984). Properties of cutaneous mechanoreceptors in the human hand related to touch sensation. *Human Neurobiology*, 3, 3–14.
- Williams, B. A., Kay, R. F., & Kirk, E. C. (2010). New perspectives on anthropoid origins. *Proceedings of the National Academy of Sciences*, 107, 4797–4804.