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Evolution of the Special Senses in Primates

The imortance of various sensory systems to the study of primate ecology and evolution has never been disputed. However, the functional and adaptive significance of each sensory system, such as vision, olfaction, or hearing, is usually studied and discussed in isolation. The manner in which these systems function and evolve together is often ignored. To begin rectifying this, Tim Smith (Slippery Rock University), Callum Ross (Stony Brook University), and Nate Dominy (University of Chicago) organized the symposium "Evolution of the Special Senses in Primates" conducted as part of the 73rd Annual Meeting of the American Association of Physical Anthropologists in Tampa, Florida. This symposium brought together researchers in comparative neuroscience, primate ecology, primate functional morphology, and paleoprimatology with the express purpose of comparing approaches and datasets on the evolution of primate sensory modalities.

In a complementary pair of talks Jon Kaas (Vanderbilt University), and Todd Preuss (Yerkes National Primate Research Center, Emory University) discussed the evolution of mammalian visual and somatosensory cortices and the ways in which primates are unique as compared to other mammals. Although counter-examples are found, in general primates have comparatively more specialized cortical areas devoted to special neural processing. It was suggested that this is partly a result of basic constraints on cortical size and wiring. Larger cortices have greater connectivity, meaning that neurons that distribute between regions are longer and more numerous. But longer neurons require proportionally greater myelination, which decreases signal speed along the axon. This limits maximum neuron length because slow signal speed would diminish overall cortical function. In other words, large cortical areas simply run too slowly to be efficient. Instead, new, smaller cortical areas evolve that function in a manner similar to parallel processing in computing: Complex computations are distributed among multiple subunits that individually process a portion of the computation. Therefore, each smaller unit can run more quickly. However, in addition to speeding up computation time in the brain, the evolution of new cortical areas opens the possibility that these new areas can add functions or evolve entirely novel functions. One possible interpretation of this is that the increase in relative brain size, a primate hallmark, may predispose primates to the evolution of new cortical functions. This stands in contrast to the more common assumption that relative brain size is the result of the evolution of new cortical functions.

A new example of evolutionary interaction among various sensory systems was presented by Yoav Gilad and colleagues (Max Planck Institute for Evolutionary Anthropology) on the relationship between olfactory receptor gene function and trichromatic color vision. Interestingly, they found that the platyrrhine *Alouatta,* as well as catarrhines, have proportionally more pseudogenes (nonfunctional copies of or close relatives to genes in genomic DNA) in the olfactory receptor gene family than do other platyrrhines and *Lemur catta*. The assumption is that these taxa have reduced olfactory sensitivity or at least a truncated range of odor sensitivity. These taxa with proportionally higher pseudogenes are also those that are routinely trichromatic. Full trichromacy probably evolved convergently in catarrhines and *Alouatta,* suggesting that the pseudogenes that decrease olfactory receptor function also evolved convergently. The causal link, if any, between olfactory pseusogene evolution and routine trichromacy is unclear. It is also unclear why trichromats may rely so little on olfactory function.

Eliot Bush and John Allman (Caltech) with Elwyn Simons (Duke University) presented data on brain component volumes derived from CT analyses of the new and remarkably complete skull of *Parapithecus grangeri*. Comparative scaling suggests that *Parapithecus* resembled modern strepsirrhines in relative brain size and in the volume of the olfactory bulb relative to overall brain volume. The area of the optic foramen in *Parapithecus,* a rough surrogate of retinal ganglion axon number, scaled between strepsirrhines and anthropoids. Taken together, these results suggest that parapithecids were surprisingly primitive in comparative sensory function. Interpreting these data in light of character evolution among early anthropoids is difficult because the phylogenetic position of parapithecids is disputed. Nevertheless, the *Parapithecus* data show that several sensory traits that are characteristic of anthropoids evolved in mosaic fashion.

Mark Coleman (Stony Brook University) contributed to the discussion on primate hearing by specifically addressing the role of the outer ear, or pinna, in amplifying sound. Coleman investigated like-sized lorisoids and platyrrhines, finding that they tend to follow one of two major patterns: in strepsirrhines a relatively large pinna with a tall, narrow shape and, in anthropoids, a relatively smaller auricle

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that is more equal in height and shape. Coleman's analysis revealed that wider pinnae are more sensitive to low-frequency sounds than are narrow pinnae. However, Coleman suggested that differences in pinna morphology are probably not the only explanation for the increase in low-frequency sensitivity seen in anthropoids: The ear canal itself may play a more important role in acoustic amplification. Interestingly, activity pattern was not found to be a significant factor in this study, despite the fact that strepsirrhines are predominantly nocturnal and that anthropoids, except for the nocturnal *Aotus,* are all diurnal.

Christopher Heesy (New York College of Osteopathic Medicine) pointed out that while it is assumed that orbit convergence, a defining trait of primates, is correlated with binocular field overlap, this question has not yet been directly investigated. Owls, for example, possess forward-facing eyes but, surprisingly, exhibit less than 45 degrees of binocular field overlap. Mammals display considerable diversity in both orbital convergence and binocular field overlap, from animals such as horses, which have laterally facing orbits and very little binocular field overlap, to primates, which have extremely convergent orbits and a large field of binocular overlap. Heesy combined his own data on mammal orbit convergence with data on all mammals for which binocular field overlap has been measured. His analysis revealed a strong linear relationship between the two variables, confirming long-held assumptions of mammal visual ecology.

Charles Wysocki (Monell Chemical Senses Center) provided an interesting addition to the discussion on olfaction in primates by presenting a study on human pheromones entitled "Human chemical communication: Should we fearamone?" It is often assumed that effective chemosensation requires a functioning vomeronasal organ, which is not present in modern humans. However, Wysocki argues, it is not necessarily the case that a vomeronasal organ is required, and it may be that human pheromones function in a way that has not yet been identified. This study obtained pheromones from the axillae of adult men and noted the response of adult women exposed to the scent. Contrary to common belief (as shown by a thriving Internet market that sells "pheromones" in liquid form), the presence of male pheromones does not elicit a sexual response in women. However, the women did report a mild response of feeling secure and relaxed after smelling the pheromones. It is also apparent that pheromones are virtually unstudied in nonhuman primates.

Nate Dominy (University of Chicago) ended the session on primate sensory systems by discussing touch, a sense not covered in any other contribution. Dominy pointed out that no one sense is solely responsible for which food items are consumed and which are rejected, and that this decision-making process usually involves a complex interplay between senses. It is often assumed that primates rely primarily on vision to determine fruit edibility. However, color alone is a poor predictor of sugar content, the primary nutritional component of fruit. Dominy suggests that instead olfaction may cue an animal to which fruits in a bunch are the most likely to be ripe, and then palpation will convey important information about a food item's elasticity and, therefore, its quality. Dominy showed a video clip of a chimpanzee confronted with a bunch of figs that were individually indistinguishable by eye, being a uniform green color. The animal used palpation to decide whether to consume or discard several pieces of the fruit, implying that there is a cognitive link between knowledge of texture and food desirability.

The most valuable result of this symposium was that it illustrated that an integrated approach would make a strong research program for the future. Primates certainly combine these systems for sensory information. The level of knowledge is such that we can now combine methods from different subfields of primatology with comparative neuroscience to achieve a better understanding of the evolution of primate sensory systems.

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