1 Primates as Auditory Specialists

Asif A. Ghazanfar and Laurie R. Santos

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I. INTRODUCTION

A brief survey of the animal kingdom quickly reveals an impressive array of sensory specializations, each engineered to solve a particular type of adaptive problem. Such a diverse collection of adaptive specializations is especially prevalent in the auditory domain. Acoustic engineers would likely be impressed by the diverse solutions different animals have found to the problems of sound localization, auditory discrimination, and vocal recognition. Echolocating bats, for example, have an auditory system exquisitely tuned for nocturnal prey catching. They are able to use the difference between the sound of an emitted vocalization and its subsequent echo to identify and localize moving targets in a dark environment. Similarly, the auditory systems of many anuran and avian species are specifically tuned for recognizing mating calls and other conspecific vocalizations.

Unfortunately, when one thinks of the impressive auditory specializations of the animal kingdom, one rarely considers those of animals within the primate order. Although human primates clearly possess specialized mechanisms for processing speech, few consider the auditory systems of other primate species to be exemplary
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in any way. In fact, while many consider primate auditory systems to be important and effective models of general auditory processing, few auditory physiologists would describe these systems as particularly specialized for species-specific ecological problems or as masterfully designed as those of bats and anurans.

This species-general view of primate audition is incorrect and, more importantly, detrimental to a rich understanding of the structure and function of primate auditory mechanisms. We hypothesize that the design of primate auditory circuitry, like that of other taxa, reflects the specialized functions that these systems have evolved to carry out. In this chapter, we review the ways in which primates naturally use their auditory systems, focusing particularly on the problems of avoiding predation, locating food, and finding mates. We propose that a more thorough understanding of the adaptive nature of primate audition is necessary for neuroscientists to develop better questions about the structure and function of primate auditory mechanisms.

II. AVOIDING PREDATORS

One of the most persistent adaptive problems facing our primate ancestors was the task of avoiding potential predators. Today, most primate species serve as prey to at least one kind of predator, and many species are hunted by a number of different predator types. Red colobus monkeys (Procolobus badius), for example, are preyed upon by eagles, leopards, chimpanzees, and human poachers.1 Predation rates can often be incredibly high, and in some species predators bring about more deaths than disease, injuries, and other causes. In vervet monkeys (Cercopithecus aethiops), for example, predation alone accounts for over 70% of all deaths.2 With mortality rates as high as these, natural selection has exerted strong pressure on the evolution of antipredator tactics and, in particular, on mechanisms specialized for avoiding predators. In the auditory domain, these tactics can include the detection of predatory-specific auditory signals as well as recognition of the alarm calls of conspecifics and other sympatric species.

In response to hearing or seeing a predator, many primates produce alarm calls. More impressively, a number of primate species distinguish among various predators, producing aurally different alarm calls for different classes of predators. Perhaps the best known antipredator tactic is the alarm-calling behavior of vervet monkeys. Vervet monkeys in the Amboseli National Forest are preyed upon by at least three different predator classes: eagles, leopards, and snakes.3,4 Because each of these predators hunts in a different way, no single general-purpose antipredator tactic would be effective against all. When faced with an eagle, for example, a vervet monkey’s safest response is to hide as close to the ground as possible. When faced with a leopard, however, the ground is the most dangerous place to be; instead, vervets must immediately move as high off the ground as possible. Vervets must distinguish among different predator classes and react in a predator-appropriate way. One way vervets manage to categorize different predators is through the use of three predator-specific alarm calls, one for aerial predators, one for leopards, and one for snakes.5 Seyfarth et al.6 played these different calls back to vervet subjects and found that individuals always reacted to the calls in a predator-appropriate way. When subjects heard playbacks of leopard calls, they ran into the trees; but when they heard eagle alarm calls, they hid under bushes on the ground. These results suggest that vervets naturally distinguish between both the different predator classes and the vocalizations associated with those classes.

Conspecific alarm calls are not the only kind of acoustic information relevant for predator detection. Many primates live sympatrically with other alarm-calling primate and nonprimate species that are preyed upon by the same predators as vertebrates. As such, the ability to detect, learn, and respond adaptively to the alarm signals of heterospecific individuals would be strongly selected for during an organism’s evolutionary history. There is now much evidence to suggest that primates do just this; many primate species can learn, and respond adaptively to, the alarm calls of other species with whom they are sympatric.5,6 In southern India, for example, bonnet macaques (Macaca radiata) groups are found in association with Nilgiri langurs (Trachypithecus johnii), Hanuman langurs (Semnopithecus entellus), and sambar deer (Cervus unicolor), but the frequency of such associations varies between groups of bonnet macaques. All four species fall prey to leopards and produce alarm calls upon detecting a leopard. Ramakrishnan and Coss7 compared the responses of bonnet macaques to playbacks of conspecific alarm calls with playbacks of alarm calls of the other three species. They found that there are differences in the latencies to flee following conspecific vs. heterospecific alarm calls. Thus, bonnet macaques treated the heterospecific alarm calls with as much urgency as they would a conspecific alarm call. On a group-by-group basis, however, the responses to alarm calls of species to which bonnet macaques were not frequently exposed were significantly different from the responses to their conspecific alarm calls. This suggests that sufficient experience is necessary for bonnet macaques to learn the alarm calls of other species and argues against the idea that the responses are driven solely by the acoustic features of alarm calls in general (for similar results in Diana and Campbell’s monkeys, see Chapter 2).

The ability to learn a secondary cue for danger, such as the alarm vocalizations of another species, may be a capacity specific to the auditory domain. While primates seem to readily learn the secondary auditory cues of danger (e.g., the alarm calls of other species or the sounds that predators themselves make), there is scant evidence that they understand secondary visual cues of danger. Cheney and Seyfarth8 tested whether vervet monkeys knew enough about the behavior of leopards to understand that a carcass in a tree in the absence of a leopard represented the same potential danger as did the leopard itself. A stuffed carcass of a gazelle was positioned up in a tree. When vervets saw the carcass, none produced alarm calls or showed any increased vigilance behavior. Thus, despite the experience vervets have with seeing leopards and their prey together in trees, they did not behave as though the carcass might mean that a leopard was nearby. A similar experiment was conducted for another predator class. Could vervets associate the distinctive tracks of a python with the possible presence of the python itself? Pythons prey upon vervets frequently, and vervets readily alarm call upon seeing a python. Yet, upon seeing fresh python tracks, vervets did not alarm call or increase their vigilance. In stark contrast, vervets readily respond to the alarm calls of starlings, a secondary auditory cue for the presence of terrestrial and aerial predators.5,6

Cheney and Seyfarth8 have argued that vervets’ inability to adaptively use secondary visual cues of predators may be related to their limited use of visual signals...
as secondary cues in their social interactions. In the auditory domain, however, vervets regularly use auditory signals to designate objects or events, and this may facilitate their use of auditory signals as cues when dealing with other species.

III. FINDING FOOD

Predator avoidance is not the only significant adaptive problem that all primates must face. In order to survive, primates, like other organisms, must forage for food. At a proximate level, a primate’s size and food processing apparatus (i.e., its teeth and gut) constrain its food choices. Although the diet of a given primate can be diverse enough to include insects, fruits, leaves, vines, nectar, sap, and resin, most primates are easily classified according to the food type they most commonly eat. The five main dietary classes are insectivores, nectarivores (gums and sap), frugivores (fruits), graminivores (seeds), and folivores (leaves). These dietary variations among species can often be related to morphological and physiological differences. For example, within the Callithrictidae, maroon (Callithrix jaccus and Callithrix cebuella) have long, forward-projecting lower incisors consistent with their nectarivory (necessary to gouge holes in tree trunks), while tamarins (Saguinus and Leontopithecus), like most primates, do not have such a dental adaptation. A more familiar food-related adaptation is cheek pouches, typically used by Cercopithecinae for their "retrieve-and-reterrret" pattern of feeding. Such a tactic is useful in situations where competition from conspecifics is intense and for the enzymatic predigestion of food. Specialized adaptations for feeding and foraging should be no less prevalent in the auditory system. In this section, we consider the relationship between perceptual specializations in the auditory domains and the foraging behaviors of different primates.

A. DIRECT AUDITORY CUES

The two categories of auditory cues that primates can use to detect food are direct and indirect. Direct cues include the sounds of prey or self-generated acoustic cues that could be used to identify where prey might be found. Indirect auditory cues include the calls of conspecifics or other sympatric species that could lead a listener to the location of a food source.

The use of direct auditory cues can sometimes be related to the anatomy of the ears. For example, many insectivorous nocturnal primates have large, membranous outer ears that can be moved in several directions. The prosimian aye-aye (Daubentonina madagascensis), for example, uses its large ears to detect larvae that reside in wood cavities. By tapping on wood surfaces with its long middle finger, they seem to detect cavities made by insects by changes in the reverberation of sound. Such detection is, without a doubt, aided by their large ears. Another prosimian, the galago (Galago demidovii and Eutocius elegantulus), locates scurrying or flying insects primarily by the sounds these prey make. A cricket can escape detection as long as it remains quiet and immobile; however, as soon as it moves or makes a sound, a galago will move its ears in the appropriate direction to locate the prey and then grasp it, often in mid-air. Indeed, experiments in which insects were placed behind a plywood screen revealed that galagos followed the movements of insects with precise head movements, almost as if they can see the prey. Direct auditory cues are also used by chimpanzees (Pan troglodytes) when they hunt monkey prey. In the dense forest, chimpanzees detect their preferred prey species, the red colobus monkey (Procolobus badius), by the colobus' frequent vocalizations. Red colobus monkeys are very vocal, especially compared to sympatric primates, and, naturally, one of their antipredator strategies upon hearing chimpanzees is to reduce their vocalization rates.

B. INDIRECT AUDITORY CUES

Food-associated vocalizations — indirect auditory cues — are produced by many New and Old World primates. These calls can let receivers know the location and characteristics of a food source. Depending on the species, characteristics such as quantity, quality, and divisibility can be indicated by the probability and rate of food calling by the discoverer. For example, toque macaques (Macaca sinica) produce special food calls when they discover a new location of food. It is the quantity (must be large), not the food type, that seems to elicit calls from the discoverers. In other words, the same food but in low quantities does not elicit food calls from toque macaques. Upon hearing food calls, dispersed receivers immediately run to the site and feed there. These calls, therefore, convey information about the presence of a food source, its location, and its quantity.

Rhesus macaques (Macaca mulatta) produce three different calls (chirps, warbles, and harmonic arches) associated exclusively with the discovery of preferred, rare foods (e.g., coconuts, berries, etc.). The rate of calling is positively correlated with the hunger level of the caller. When conspecifics hear these calls, they typically approach the caller. Interestingly, all members of a given rhesus monkey troop do not call with equal probability upon discovering high-quality foods. Adult males are less likely to produce food calls compared to adult females, and among those who do call they are more likely to be residents of the group than peripheral males. Among females, those within large matriline are more likely to produce food calls compared to females in smaller matriline. What happens when a rhesus monkey finds good food and fails to give a food call? If such cheating is discovered by a conspecific, the result is increased aggression from group members, regardless of the cheater’s rank.

In cotton-top tamarins (Saguinus oedipus), a New World monkey, food calling may serve slightly different functions and may depend on social conditions. Tamarin social groups include a stable, monogamous pair with one or more generations of offspring. They produce two calls in their repertoire that are exclusively associated with food-related activities: the C-chirp and the D-chirp. C-chirps are produced as they approach a food source, and D-chirps are produced during feeding. In a series of experiments on captive cotton-top tamarins, Roush and Snowdon tested the influence of food types, food quantity, food distribution, and audience effects on food calling rates. While neither food quantity nor distribution affects the calling rate, adult mate-pairs call at a higher rate than immature individuals or mate-pairs. The presence or absence of a mate-pair in the vicinity of the food has no effect on food calling rates among discoverers, suggesting that there is no
IV. FINDING (AND KEEPING) A MATE

A. Copulation Calls

Although avoiding predators and locating food are essential tasks for survival, a primate’s ultimate reproductive success requires finding high-quality mates. In a wide variety of mating systems, mate choice is based on an assessment of auditory signals presumed to correlate with fitness. For example, for one species of frog (Physalaemus pustulosus), the fundamental frequency of the male advertisement call (which correlates positively with body size) is used by females to select the biggest male as a mate. In another species of frog (Hyla versicolor), the duration of the advertisement call is used as an indicator of male genetic quality; longer duration calls are preferred by females, and males with the longest calls sire the fittest offspring.

In many Old World monkey and ape species, particularly those with multi-male mating systems, individuals (males, females, or both sexes) produce copulation calls. These calls are produced immediately before, immediately after, or during copulation and serve as auditory cues for reproductive status. In rhesus monkeys, only males produce copulation calls and always during copulation. Whether or not their production is under voluntary control, they could be used as indicators of male quality. Three pieces of evidence support this idea. First, the number of calling males decreases with increased competition for estrous females. Second, males, independent of rank, who produce copulation calls receive more aggression from conspecifics. Finally, copulation-calling males have a greater mating success (in terms of number of copulations) than silent males. In essence, males who call are more fit because they can withstand the aggression of other males following their copulation calls. However, it is not known whether females show preferences among the males who do call or what acoustic features they might be using as cues.

Semple has studied the function of female copulation calls in Barbary macaques (Macaca sylvanus). Following playbacks of their copulation calls, Barbary macaque females were mated sooner than following a control playback. Playbacks to male dyads revealed that only the higher ranking of the two would approach the sound source, while the other male stayed behind. These results suggest that these Barbary macaque copulation calls provide an indirect mechanism of female choice (because females end up with the higher ranking male more often) and promote sperm competition by reducing the interval between matings. Of course, a male Barbary macaque looking for a suitable mate would be wise to select, and fight for, a mate who is at the peak stage of fertility. Indeed, male Barbary macaques can actually distinguish the reproductive states of conspecific females based on voice alone. Playbacks of female copulation calls produced during late estrus (when she is most likely to ovulate) elicited stronger responses from males than calls produced during early estrus. The dominant frequency and/or the duration of the copulation call are two acoustic cues males may use to discern the reproductive states of females. Late estrus calls had longer durations and higher dominant frequencies than early estrus calls. Taken together, the data from both rhesus and Barbary macaques suggest that these primates can and do use copulation calls to influence their reproductive success.

B. PRIMATE SONGS

Singing has evolved four times in the primate lineage and is represented by 26 species of primates. All of them have monogamous mating systems. What is a primate song? Like birdsong, it is defined as a concatenation of different notes that together form a recognizable pattern over time; they can last for several tens of minutes. Both males and females can sing in some species, and sometimes they sing together in duets. Also like birdsong, primate songs are thought to have two main functions: to defend territories and to strengthen pair bonds. For strengthening pair bonds, there has been scant supporting evidence, but recent studies of gibbon singing have provided some new insights.

Geissman and colleagues studied the duet songs of one species of gibbon, the siamang (Hylobates syndactylus). Duet songs are mostly produced by mated pairs and are exquisitely timed vocal exchanges between mates using components of their individual songs. As a male sings his song, the female will insert, at regular intervals, long parts of her song. How does each member of the pair know when to start and stop singing? If such song coordination had to be learned (an investment of time and energy), then this would support the idea that singing (and duetting, in particular) can function to strengthen pair bonds. To test this idea, the changes in duet structure were examined for two pairs of siamangs during a forced partner exchange. When the new pairs formed, they had difficulties in synchronizing their duets and produced atypical (relative to their song behavior before the partner exchange) sequences of calls. Thereafter, the two newly formed pairs showed changes in their duetting behavior that can only be interpreted as a learning effort: one partner would adapt its singing behavior to compensate for the mate’s song structure. For example, a male in one pair dropped the last syllable of one of his songs so that it did not overlap with a similar sounding syllable sung by the female.