Flexible usage and social function in primate vocalizations

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Vocalizations are a pervasive feature of nonhuman primate social life, yet we know surprisingly little about their function. We review studies supporting the hypothesis that many primate vocalizations function to facilitate social interactions by reducing uncertainty about the signaler's intentions and likely behavior. Such interactions help to establish and maintain the social bonds that increase reproductive success. Compared with humans, songbirds, and a few other mammals, primates have small vocal repertoires that show little acoustic modification during development. However, their ability to modify call usage is extensive and tuned to variation in the social context, including the historical relationship between caller and listener and the caller's assessment of how a listener is likely to respond. We suggest parallels between the decision to vocalize and neurophysiological studies of other, nonvocal social decisions between interacting monkeys. The selective factors driving the early stages of language evolution may have come from the need to make decisions about when and how to call within the context of social challenges.

vocalizations | nonhuman primates | vocal usage | social behavior | cognition

Despite decades of research on nonhuman primate vocal communication, we still know little about the causal mechanisms that underlie vocal production and surprisingly little about its function. These gaps in our knowledge are especially striking compared with the progress that has been made in understanding the function of other common social behaviors. In particular, there is now considerable evidence from a variety of nonhuman primates that social bonds are adaptive: individuals who maintain close, enduring bonds with others live longer and experience greater reproductive success (1–4). Measures of bond strength have incorporated a variety of behaviors, most notably grooming, proximity, and alliance formation (e.g., refs. 1, 2, and 5–8). Few, however, have included vocalizations (but see ref. 9). The implicit assumptions seem to be that nonvocal behaviors are sufficient to characterize the strength and quality of relationships and that vocalizations are redundant or perhaps even irrelevant.

This omission is puzzling because vocalizations are a pervasive feature of primate social life. Most primates vocalize far more often than they groom or form alliances. If vocalizations contribute little to a factor strongly associated with fitness—close social bonds—why do primates vocalize at all?

Mammals exhibit considerable flexibility in their ability to learn novel calls. Dogs, for example, can learn to associate human words with specific objects and actions (10). Similarly, primates can learn to recognize almost any sound-meaning association, including other species' alarm (11, 12) and social calls (13). When responding to conspecifics' calls during social interactions, primates take into account a variety of social and contextual contingencies, including the identity of the signaler, the type of call given, the nature of recent interactions with the signaler or one of the signaler's close associates, and the recipient's apparent knowledge

of the correlation between past and future interactions (reviewed in refs. 14–16). For example, after receiving aggression from a higher-ranking female, female chacma baboons (*Papio cynocephalus ursinus*) respond to the threat-grunt of a close relative of their opponent as if it constitutes a vocal alliance signaling possible renewed aggression, and they avoid both the original opponent and her relative (17). Subjects show little reaction, however, to the threat-grunt of a female unrelated to the opponent. Conversely, if subjects hear the "reconciliatory" grunt of a close relative of their opponent, they are more likely both to approach their former opponent and to tolerate the opponent's approaches. No such reconciliatory effect occurs if a subject hears the grunt of a female unrelated to her opponent (18). Similarly, in playback experiments on wild chimpanzees (*Pan troglodytes*), males were more likely to avoid the aggressive barks of a former opponent's close associate than the aggressive barks of a nonassociate (19). The recognition of other individuals' close associates may be especially important for male chimpanzees, who can improve their dominance rank, and hence reproductive success, by forming coalitions with other males (7).

Communication is inherently social, involving both a producer and at least one perceiver. Since perceivers are also signalers, one might expect that similar mechanisms would underlie call production and perception. This seems not to be the case, however. As Darwin noted in 1871, animals like dogs may recognize many human words but their vocal repertoires are limited and appear primarily to reflect underlying emotional states (20). Consistent with this view, learned, flexible vocal production is relatively rare in animals, appearing in only a few orders of birds

Significance

When compared with humans, nonhuman primates have small vocal repertoires that show little acoustic modification during development. These limitations pose a dilemma for those interested in the evolution of language. Recent research, however, suggests that monkeys and apes show an extensive ability to modify their use of calls in different social contexts. Many vocalizations function to facilitate social interaction by reducing the uncertainty about the signaler's intentions and likely behavior. Such interactions help to establish and maintain the social bonds that increase reproductive success. For scientists interested in the evolutionary transition from non-linguistic communication to language, a logical starting point should be social interactions between long-lived individuals who interact repeatedly and for whom long-term social bonds are of paramount importance.

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and a small number of mammals, including humans (21). Compared with humans, nonhuman primates have a limited vocal repertoire of calls that are predictably linked to specific social contexts and show little acoustic modification during development (22, 23).

Within these constraints, however, there is considerable flexibility in call usage. Studies of group-living animals have shown that variation in vocal output—in particular the decision to call or remain silent—depends on a multitude of contextual cues, including the identity of potential listeners and the caller's relationship with them (e.g., refs. 15, 24, and 25). The difference between constrained call acoustics and flexible call usage led Janik and Slater (21) to distinguish between production learning, which is rare in most mammals, and usage learning, which is common.

Here, we describe some recent examples of flexible call usage in the vocal behavior of nonhuman primates. We review evidence supporting the hypothesis that, in social groups of long-lived individuals, vocalizations are adaptive in part because they serve as honest indicators of the caller's intentions. We suggest that, whereas the acoustics of call production are highly constrained, primates exhibit a flexibility in call usage that is similar to the flexibility that they display when responding to the calls of others. Finally, we briefly discuss some of the neural mechanisms that might underlie flexible call usage and consider more broadly the relation between social signaling and social cognition.

Social and Motivational Correlates of Vocal Production

It has long been known that variation in alarm calling in many mammalian and avian species is subject to audience effects. Individuals are more likely to produce alarm calls when in proximity to others than when alone, and when in the presence of kin or close associates than in the presence of nonkin (vervet monkeys, *Chlorocebus pythygerus*: ref. 26; chimpanzees: refs. 27 and 28; see ref. 29 for review). The same appears to be true of other loud, long-distance calls, including food and contact calls. Chimpanzees, for example, are more likely to produce food calls in response to the simulated arrival of a friend than a nonfriend (30), suggesting that food calls can be selectively withheld or emitted in different contexts. Both Japanese macaques (*Macaca fuscata*) and ring-tailed lemurs (*Lemur catta*) are more likely to respond to the contact calls of a close grooming partner than to the calls of a less closely bonded individual (9, 31). Similarly, female baboons selectively respond to their close relatives' long-distance contact barks (32).

More commonly, vocalizations are produced at close range and during social interactions. Strikingly, these close-range calls appear to serve a function that is distinct from that played by other affiliative behaviors like grooming. Rather than reflecting existing social bonds, close-range calls seem instead to facilitate social interactions by reducing uncertainty between partners who might not otherwise interact often.

As Silk et al. (33) and Searcy and Nowicki (34) have pointed out, whenever two animals come together there is uncertainty about the outcome because the best strategy for one depends upon what the other does, and vice versa. If the individuals involved are strangers or competitors whose interests do not overlap, they may try to bluff or deceive their opponent about their condition or likelihood of attack, giving rise to the hypothesis that deceptive or manipulative signals should be evolutionarily stable (35, 36). In many social groups, however, individuals interact repeatedly, thus reducing the effectiveness of unreliable signals. Because animals in many species "eavesdrop" on other individuals' behavior (37), individuals who consistently signal unreliably about their intentions are soon ignored or challenged. As a result, signals given during competitive interactions are usually accurate (33).

Equally important, animals living in the same social group often have overlapping interests—not just in reducing uncertainty during the immediate interaction, but also in potentially enhancing a long-term social bond (16, 38). Under these conditions, honest signals that accurately predict the signaler's behavior are adaptive for both signaler and recipient because they facilitate social interactions.

As an example, consider the grunts given by female baboons and rhesus macaques (*Macaca mulatta*) when they approach one another (33, 38). The interaction has an uncertain outcome because neither female knows what the other's response will be. Low-ranking females, including mothers with attractive young infants, may be particularly nervous at the approach of a more dominant individual. Approaching females who are motivated to interact with their partner can increase the likelihood of an affiliative interaction by grunting as they approach and predictably following their grunts with friendly behavior. In both baboons and macaques, an approaching female who grunts is more likely to be friendly and less likely to be aggressive than one who remains silent. The predictable relation between grunting and friendly behavior enhances the likelihood of an affiliative interaction because subordinate females are less likely to move away from an approaching female when she grunts than when she remains silent (33, 38). Both females benefit from recognizing the contingency between grunting and subsequent behavior because both females benefit from the subsequent interaction. In baboons, grunts also serve a reconciliatory function. Grunts by the aggressor shortly after a conflict make it less likely that the conflict will continue and more likely that the victim will approach her former aggressor (39, 40, 41).

Silk et al. (33) show that low-cost, honest signaling can evolve even when there is some degree of conflict between the animals involved. They note that such signaling is particularly likely to become evolutionarily stable when coordination between partners is valued and animals interact repeatedly over time. This conclusion is important because these are just the conditions that exist in most primate groups, and indeed in many other groups of birds and mammals.

Baboon grunts do not function just to reinforce existing social bonds; baboons are not simply "vocal grooming" (42). Instead, baboons use grunts strategically, grunting when calls play an important role in facilitating social interactions and remaining silent when such calls have little impact or there is less uncertainty about the probable outcome of an interaction. Females are more likely to grunt if their partner is lower ranking or has a young infant. Conversely, they are substantially less likely to grunt when they approach their own mothers or daughters—the individuals with whom they share the closest and most predictable bonds—than when they approach others (43).

The low likelihood of grunting between mothers and daughters may reflect the fact that grunts play a smaller role in mediating their interactions than grunts between other females do. In the absence of grunts, mothers and daughters are more likely to behave affiliatively and less likely to behave aggressively than other pairs of females, perhaps mitigating the need for signals of benign intent. This pattern, however, holds only for mothers and daughters; notably, patterns of grunting between sisters are similar to those among nonkin. Although social bonds between sisters are significantly stronger than those between less closely related individuals, their rates of aggression are similar to those among nonkin (44). Thus, when one sister approaches another there is some uncertainty about whether her subsequent behavior will be friendly or aggressive. Grunts to sisters, like grunts to unrelated females, may function to reduce uncertainty by signaling the approaching sister's low likelihood of aggression. Supporting this hypothesis, sisters whose relationship is more aggressive are more likely to grunt to each other than sisters whose relationship is less aggressive (43).

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Social groups of animals contain individuals with different reproductive interests and competitive abilities. Nonetheless, group members are able to synchronize their activities, coordinate travel, and maintain social relationships that include both cooperative and competitive elements. Vocal signals play an important role in this process. Unlike grooming, which is typically concentrated among a relatively small subset of individuals (e.g., ref. 44), vocalizations like grunts are given to almost every individual, including those with whom the caller does not interact often. Under these ambiguous circumstances, both the production and the perception of grunts rely on individuals' recognition of a predictable relation between vocalizations and subsequent behavior. Honest, low-cost signals like baboon grunts have evolved, at least in part, to resolve this uncertainty (33).

The strategic use of vocalizations that have subtly different effects on behavior is widespread among primates. Flexible vocal behavior, moreover, takes many forms. It can include the combination of different call types (e.g., refs. 45 and 46), the subtle acoustic modification of calls (e.g., refs. 25, 47, and 48), or the adoption of novel call types (e.g., ref. 49 and 50) in different social or ecological contexts. Bonobos (*Pan paniscus*) provide one example.

Bonobos live in fluid parties of varying size and composition (51). Their fission–fusion society creates some uncertainty for individuals attempting to leave their current foraging party, join another, coordinate movement between parties, or more generally maintain relationships with others who may be out of sight. To facilitate interactions, bonobos use several distinct vocalizations, given either singly, in combination, or in "conversational" exchanges. The most common call is a "high hoot" (HH) that appears to function as a general contact call. HHs given alone generally elicit no reply from individuals in nearby parties and do not predict subsequent movement by either the caller or listeners. Occasionally, however, a caller combines a HH with a second call. When this combination includes a "whistle" (W+HH), the caller is significantly more likely to leave his current foraging party and join another. His decision to join is also influenced by whether or not his W+HH is answered by a member of the party that the caller joins. Joining is significantly more likely if the W+HH is answered with another W+HH (52). Moreover, callers appear to vary the acoustic structure of whistles depending on whether or not they are given spontaneously or in response to another individual's W+HH (52). By contrast, if a HH is combined with a "low hoot" (LH+HH), the caller rarely moves to another party. Instead, a LH+HH is followed by a significant increase in the likelihood that the caller's party will be joined by an individual from another party, regardless of whether the LH+HH is answered (53).

As in the case of baboon grunts, bonobos' use of call combinations appears to function to reduce uncertainty about the caller's intentions and subsequent behavior. HHs alone undoubtedly play an important role in interparty communication and travel coordination (54, 55). However, given their use across many different contexts, it is likely that, without additional contextual cues, HHs alone provide listeners with only ambiguous information. By combining HHs with Ws or LHs, bonobos reduce ambiguity by signaling to listeners their motivation either to join another party or to recruit others to their own party. Furthermore, by varying the acoustic structure of whistles, signalers distinguish between calls given spontaneously or in response. In the unpredictable context of fission–fusion travel coordination—will A move to B or vice versa?—calls that reduce uncertainty may benefit both callers and receivers by facilitating reunions that are necessary to maintain social relationships.

To date, there is little evidence that nonhuman primates take into account their audience's mental states when producing calls. Although call usage appears to be influenced by the signaler's inferences about the listener's likely behavior, it does not seem to be influenced by inferences about the listener's state of ignorance or knowledge (38). Although baboons, for example, selectively answer the contact barks of their close relatives, their likelihood of calling appears to be influenced more by their own state of separation from the group than by that of their relatives (32). Similarly, females' production of "reconciliatory" grunts following aggression seems to be prompted more by their own motivation to resume friendly interactions with their opponent than by any concern for their opponent's level of anxiety (39, 40).

Even in the case of chimpanzees, evidence for mental state attribution during call production is mixed. In two independent experiments in which wild chimpanzees were presented with snake models, subjects gave more "alert hoos" when bystanders were ignorant of the snake's location than when they had already seen it, but the degree to which callers were influenced by the bystanders' behavior and by habituation effects was not clear (27, 28).

In a more recent experiment designed to control for these potential confounds, a chimpanzee encountered a snake model in its path just after it had heard a playback recording of either the alert hoo from a second group member (simulating that the other individual had also detected the snake) or a "rest hoo" from the same individual (indicating, presumably, that it had not). Subjects were more likely to give alert hoos in the second case. Importantly, subjects in the second case were also more likely to look back and forth between the snake and the location of the putative caller. One explanation for this "marking" behavior is that subjects attributed ignorance to the putative caller after it had given a rest hoo, but not after it had given an alert hoo, and were attempting to signal the snake's location to the new arrival (56). If true, chimpanzees' calling behavior might be influenced to some degree by inferences about the listener's state of knowledge. Additional experiments will be essential to resolve this question.

Mechanisms

Authors comparing vocal communication in human and nonhuman primates have often concluded that the former is learned and voluntary whereas the latter is involuntary, unlearned, and reflexive (e.g., refs. 57 and 58). This dichotomy is not entirely accurate (14, 59). In the acoustics of call production, nonhuman primates are indeed constrained: monkeys and apes seem incapable of learning entirely new calls or engaging in vocal imitation. They can make subtle modifications of a call's acoustic structure depending upon experience (e.g., ref. 25, 47 and 48), but these are best described as minor modifications, particularly compared with the flexible phonation found in humans.

In other respects, however, call production is more flexible. In laboratory experiments, call production, the timing of call delivery, and even the production of different call types can be conditioned through reinforcement (60–62). And, as illustrated by the studies of baboons, bonobos, and chimpanzees reviewed above, primates can give or withhold vocalizations depending on the presence, identity, or behavior of their audience, as well as their history of interaction with the audience or the audience's close associates. Because it depends so clearly on a signaler's prior interactions with specific other individuals, flexible call usage is best understood as the result of learning, memory, and experience.

Although early research emphasized differences between humans and nonhuman primates in vocal tract anatomy (63), more recent analyses reveal greater homology (64), including evidence that the macaque vocal tract is capable of producing a range of speech-like sounds (65). Limited variability in the acoustic properties of primate vocalizations may therefore stem not from limitations in their vocal apparatus but from limitations in the neural circuitry needed for sophisticated vocal control (65). Humans, for example, have direct brain projections from lateral motor control areas to laryngeal motor neurons—projections that are absent in nonhuman primates and may explain their

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inability to produce new sounds (66). A comparison of human and nonhuman primate vocalizations thus reveals both continuities and discontinuities: continuities in the ability to call or remain silent and to modify the timing of vocalization in different social situations and discontinuities in the ability to produce new sounds, make major modifications in call acoustics, and engage in vocal imitation (see refs. 14, 59, and 65 for further discussion).

In virtually all nonhuman primates, different call types are predictably associated with broadly defined social contexts. This observation has led some to propose that acoustically similar calls reflect similar affective or emotional states (23, 67, 68). There is little empirical evidence for this hypothesis, however. To cite one well-known example, vervet monkeys give acoustically different alarm calls to leopards, eagles, and snakes (69, 70), but acoustically similar (although subtly different) calls to snakes, members of their own group, and members of other groups (71, 72). We have no independent evidence, however, that neural or emotional states in the latter three cases are more alike than those in the former three. Further complicating matters, vervets produce three acoustically distinct calls—grunts, "wrrs," and "chutters"—during intergroup interactions (73), arguing against the hypothesis that the "emotions" in a particular context have an obligatory link to calls with specific acoustic properties. Moreover, in habituation/dishabituation experiments, vervet listeners treat wrrs and chutters as providing similar information, since habituation to one produces habituation to the other (73, 74). In sum, although the acoustic structure of primate calls is highly conserved, there is no easy correspondence between a call's acoustic features and the neural and/or emotional mechanisms that underlie it.

Given that the acoustic structure of nonhuman primate calls is highly constrained, what are the mechanisms that underlie call usage, which is considerably more flexible and depends primarily on social factors? There is now considerable evidence that the assessment of social variables has played a major role in the common evolutionary history of human and nonhuman primates. For example, human and nonhuman primates possess homologous mechanisms for the recognition of faces (75, 76), voices (77, 78), and objects (79); the multisensory integration of voices and facial expressions (80, 81); the processing of auditory sequences (82, 83); and the analysis of social interactions (84). They also share similar mechanisms for processing the type, importance, and value of social information (85). These shared mechanisms are unlikely to have arisen by accident. Instead, they suggest that, during the long evolutionary history of human and nonhuman primates, natural selection has acted with particular force to favor skill in making social assessments. With this social perspective in mind, we focus on recent studies that combine neurophysiological recordings with observation of behavioral decisions—including the decision to vocalize—made by individuals who are interacting with each other.

Monkeys appear to be inherently biased to search for social cues when assessing other individuals' calls. When rhesus macaques hear another monkey's calls, they exhibit neural activity not only in areas associated with auditory processing but also in higher-order visual areas (86). Cells in the auditory cortex are more responsive to videos of calling monkeys than to auditory or visual signals presented separately (87). Furthermore, the effect of cross-modal presentation is greater when monkeys hear grunts than when they hear coos, possibly because grunts are usually directed toward specific individuals, whereas coos are often broadcast to the group at large (87). The greater cross-modal integration in the processing of grunts may arise because listeners must assess the social context and determine whether or not the call is directed at them (38).

In humans, activity in the anterior cingulate cortex (ACC) contributes to social decisions and may mediate complex social functions like empathy and theory of mind (85). Comparable neural mechanisms appear to be at work in the social decisions of nonhuman primates. For example, in one study in which male rhesus macaques made decisions to reward or withhold a reward from another monkey, ACC neurons selectively encoded the rewarding experiences of the recipient monkey, either responding only when monkeys chose to reward the recipient or responding equivalently to giving and receiving a reward (85, 88). In another study, rhesus macaques played an iterated prisoner's dilemma game in which they chose between defecting and receiving a certain, small reward or cooperating and receiving an uncertain, larger reward. Some neurons in the ACC selectively responded to the monkey's own choice, some responded to the partner's choice, while a third subset responded in anticipation of the partner's yet-unknown choice, as if the monkey were attempting to predict his partner's intentions (89, 90).

Similar neural mechanisms may underlie monkeys' decisions to vocalize. It is well known, for example, that primate control of vocalization during operant conditioning is mediated by activity in the mediofrontal cortex, including the anterior cingulate gyrus (66). More recently, studies of marmosets (*Callithrix jacchus*) have examined the neural mechanisms underlying vocal exchanges between male and female partners (91–93). They provide evidence that a listener's decision to answer a call or remain silent can be predicted by changes in the firing rate of frontal cortex neurons even before an individual's partner has given a call. This premotor activity occurs in both the frontal and the auditory cortex (93–95). It appears to be neither sensory- nor motor-driven, but instead depends upon the social context, constituting a "social monitoring mechanism critical to conversational exchanges" (93, p. 1,036).

Under both natural and laboratory conditions, monkeys make decisions that are apparently based in part on their expectations of how others are likely to respond. A marmoset that has heard its partner call forms expectations about how the partner will respond to an answering vocalization; a bonobo that hears a W+ HH must infer what is likely to happen if he answers or not; and a female baboon approaching a mother with infant must make inferences about how the mother will react if she vocalizes or remains silent. She must also consider how other, nearby listeners will react if she vocalizes and then behaves aggressively. Like face recognition, gaze following, and the processing of social information, the decision to vocalize constitutes one of the building blocks of social behavior—skills that have been shaped by natural selection in an environment where animals recognize the contingent relations between signals and behavior, eavesdropping individuals monitor one another's actions, and social interactions are crucial to reproductive success.

Given the flexibility that primates display in the use of different calls in different contexts, and the many ways in which contextual information affects their responses to vocalizations, we are left with the puzzle of highly constrained call production. Why should an individual who can deduce an almost limitless number of meanings from others' calls, and modify the rate at which she calls to others, be constrained by a limited, relatively fixed vocal repertoire? The difference may arise in part because call production depends on mechanisms of phonation, which are largely innate, whereas comprehension depends on mechanisms of learning, including classical and operant conditioning, which are considerably more malleable. However, this explanation continues to beg a crucial question: Why has natural selection so rarely acted to favor flexible vocal production?

The mixture of constraints and flexibility in primate communication may shed light on the evolution of social cognition. Primates live in complex societies where social relationships are adaptive and navigating the social world provides the key to reproductive success (1–3, 38). Like most mammals, however, primates have a limited repertoire of communicative signals, both gestural and vocal. This combination of complex social

demands and a limited signal repertoire has created strong selective pressure to use signals wisely—by giving calls strategically, incorporating information from the social context, anticipating how listeners are likely to respond, and eavesdropping on the vocalizations of others. Flexible call usage and sophisticated social cognition help primates solve the challenges of social life despite their limited repertoire of signals.

Relevance to Theories of Language Evolution

If we assume that nonhuman primate call production is constrained by neural mechanisms rather than vocal anatomy (65), and we further assume that vocal communication in contemporary monkeys and apes offers a reasonable approximation to the communication of our prelinguistic hominoid ancestors, two conclusions follow.

First, long before language evolved, vocal communication was at its most complex during social interactions, where it served a somewhat different function from other social behaviors like grooming. For models seeking to explain the evolutionary transition from nonlinguistic communication to language, therefore, a logical starting point should be social interactions between long-lived individuals who interact repeatedly over time and for whom long-term social bonds are of paramount importance. Such vocalizations fulfill many of the criteria suggested for language precursors (96–98): they are honest, mutually beneficial to signaler and recipient, adaptive even though they comprise a small lexicon, and their usage must be learned because it depends on the learned recognition of other individuals' identities, ranks, and kinship relations. For listeners, calls denote features in the real world, in particular specific individuals interacting in particular ways (16). Of course, these early precursors may apply to vocal communication in many species, so they cannot by themselves explain the evolution of language exclusively in the human lineage (98, 99). Nonetheless, precursors are of interest wherever they are found. Data on social vocalizations suggest that the selective factors shaping the precursors of language came not from the need to build larger and larger vocabularies to label features of the external world—think of vervet alarm calls—but from the use of increasingly elaborate vocalizations to solve social challenges, communicate intentions, and reduce ambiguity and uncertainty.

Second, long before the emergence of language, brain mechanisms linked to social cognition and flexible call usage were already present: in the decision to vocalize or remain silent, to produce one call type rather than another, and to assess the social and historical context of a given social interaction. What remained was for selection to favor changes in the brain mechanisms controlling vocal learning, imitation, and modification of the acoustic fine structure of calls. Flexible call usage, and the cognitive mechanisms underlying usage, response, and the judgment of contextual factors, may have set the stage and created selection pressures leading to the evolution of learned, flexible production.

Conclusions

In nonhuman primates, the different developmental trajectories of vocal production, usage, and response to calls create an oddly asymmetric system of communication in which a small repertoire of relatively fixed calls, each linked to a particular context, can nonetheless give rise to an open-ended, highly modifiable, and cognitively rich set of meanings (15). Current evidence from a variety of sources suggests that the mechanisms underlying call usage in monkeys and apes are in some respects similar to those that underlie listeners' responses. Just as responses to calls depend on contextual factors like the caller's identity and the nature of the listener's recent interactions with the caller, an individual's decision to call or remain silent depends upon its assessment of current circumstances, including the quality of the relationship between listener and caller, the caller's current motivational state, and the caller's inferences about the listener's likely response. These assessments do not require that callers recognize mental states like ignorance in others; the decision to call or not could easily be shaped through learned contingencies. However, the complexity of social factors cannot be underestimated: like human infants trying to decipher the meaning of a word when they first hear it, a primate must decide which of many contextual cues are relevant and which are not. Despite their limited vocal repertoire, nonhuman primates appear to be skilled at modifying call usage in different social contexts.

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