



# Pragmatic flexibility in primate vocal production

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The production of vocalizations by monkeys and apes is often described as highly constrained and fundamentally different from human speech. We review recent field studies of baboons and bonobos that suggest greater flexibility. Calls function to reduce the uncertainty inherent in social interactions. Vocal production, like individuals' responses to calls, is subtly tuned to variation in the social context, including a caller's assessment of how a listener is likely to respond. We suggest parallels between the decision to vocalize and laboratory, neurophysiological tests of social decisions. We also discuss implications for theories of language evolution.

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## Introduction

Despite decades of research on non-human primate vocal communication, we still know little about the factors that cause individuals to give a vocalization. This is surprising, because we know a great deal about other common social behaviors, like grooming or the formation of alliances. In many mammals including primates, social bonds are adaptive: individuals who maintain close, enduring bonds with others live longer and experience greater reproductive success [1]. Measures of bond strength include grooming, proximity, and alliance formation. Notably, however, few studies of social relationships have included vocal communication in their assessments. The implicit assumption seems to be that non-vocal behaviors are sufficient to characterize the strength and quality of relationships, and that giving a vocalization is redundant or perhaps even irrelevant.

The omission of data on vocal production 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 the factor most closely associated with fitness — close social bonds — why vocalize at all?

Our limited understanding of call production is also striking when compared to call perception, which is known to be both nuanced and complex. Animals' responses to calls depend on many social and contextual contingencies, including the identity of the signaller, the type of call given, the nature of recent interactions with the signaller or the signaller's close associates, and the recipient's apparent knowledge of the correlation between past and future interactions [2\*,3\*,4\*]. Given that the same animals are both listeners and signallers, it seems reasonable to hypothesize that the factors affecting call production are just as complex and sophisticated as those affecting perception. Why, then, have production and perception been treated so differently?

Call production is typically assumed to be highly constrained. Primates have relatively small vocal repertoires that show little acoustic modification during development [5]. Within these constraints, however, there is considerable flexibility in call usage — the decision to call or remain silent, or to use different calls in different circumstances. Calling can be brought under operant control, and callers can modify the type of call given in different contexts [6,7]. In the wild, call usage, like responses, depends on a multitude of cues, including the identity of potential listeners and the caller's relationship with them [3\*,4\*].

Here we describe recent studies that suggest considerable flexibility in the usage of vocalizations by primates. Evidence suggests that many vocalizations function to signal the caller's intentions and to reduce uncertainty about the likely outcome of a social interaction. We briefly discuss the neural mechanisms that might underlie vocal usage and consider the implications for theories of language evolution.

## Social and motivational correlates of vocal production

Most primate vocalizations are given during close range, face-to-face interactions. Unlike other affiliative behaviors like grooming that reflect existing social bonds, close-range calls seem to facilitate social interactions and reduce uncertainty between partners who might not otherwise interact often. For example, female chacma

baboons (*Papio cynocephalus ursinus*) give low amplitude grunts as they approach other females [8]. Listeners can recognize the identity of callers based on acoustic cues [9], and can also infer whether they are the call's target from contextual cues, including the vocalizer's gaze direction and the nature of recent interactions with the vocalizer and her kin [10].

Grunts function as signals of benign intent because they accurately predict the caller's behavior. Grunts directed to lower-ranking females facilitate peaceful interactions, including grooming and infant handling. Subordinate females are less likely to move away from an approaching female when she grunts than when she remains silent [11,12]. Grunts may also serve a reconciliatory function. Grunts by an 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 [13,14].

Baboons use grunts strategically — grunting when calls play an important role in facilitating social interactions and remaining silent when the outcome is more predictable. Females are more likely to grunt if their partner is lower-ranking or has a young infant. Conversely, they are less likely to grunt when they approach their mothers or daughters — the individuals with whom they share the closest bonds [15\*].

The low likelihood of grunting among mothers and daughters may reflect the fact that grunts play a less important role in mediating their interactions than among other females. In the absence of grunts, mothers and daughters are more likely to behave affiliatively and less likely to behave aggressively than other females, perhaps mitigating the need for signals of benign intent. By contrast, 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 [16]. Thus, when one sister approaches another there is some uncertainty about whether the outcome 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 [15\*].

In sum, baboon grunts are adaptive because they reduce uncertainty and facilitate social interactions between individuals whose relationships are not always predictable [15\*,17\*]. The strategic production of vocalizations that have subtly different effects on behavior is widespread among primates. Flexible vocal behavior takes a variety of forms, including the combination of different call types (e.g. [18,19]), the subtle acoustic modification of calls

[20,21], or the evolution of novel call types [22\*,23] in different contexts. Bonobos (*Pan paniscus*) provide a recent example.

Bonobos live in fluid parties of varying size and composition [24]. 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 completely 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 generally elicit no reply from individuals in nearby parties and do not predict subsequent movement by either the caller or listeners. Alternatively, callers may combine the high hoot with a 'whistle', creating a 'whistle-high hoot' (W + HH) combination. After giving a W + HH, the caller is significantly more likely to leave his current foraging party and join another — particularly if the W + HH is answered with a HH from a member of the party that the caller joins [25\*]. By contrast, after giving a HH 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 or not [26\*].

Like baboon grunts, bonobos' use of call combinations appears to reduce uncertainty about the caller's intentions and subsequent behavior. HHs alone undoubtedly play an important role in interparty communication and travel coordination [27,28]. But 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 LHs and Ws, bonobos signal to listeners their motivation to join another party or to recruit others to their own party. In the unpredictable context of fission–fusion travel — 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. Even in the case of chimpanzees, evidence for mental state attribution during call production is mixed. In two independent experiments, a wild chimpanzee confronted a model of a snake and gave alarm calls to it. A few minutes later a bystander appeared. Although subjects gave more 'alert hoots' when bystanders appeared to be ignorant of the snake's location than when they had already seen it, alternate explanations based on the bystanders' behavior or the callers' habituation could not be ruled out [29,30].

In a subsequent experiment designed to control for these potential confounds, a chimpanzee encountered a snake model in its path. Shortly afterwards, it heard a playback recording of either the ‘alert hoo’ from a second group member (simulating that the new arrival 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 hoo 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 [31]. If true, chimpanzees’ calling behavior might be influenced to some degree by inferences about listeners’ state of knowledge.

### 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. [32,33]). This dichotomy is not entirely accurate [34,35]. 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 [5]. In other respects, however, call production is more flexible. As illustrated by the studies of baboons, bonobos, and chimpanzees reviewed above, primates can give or withhold vocalizations — or modify the type of call given — 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.

Call usage, then, depends primarily on learning, memory, and experience. This is not surprising. 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, voices, and objects; the multisensory integration of voices and facial expressions; the processing of auditory sequences; and the analysis of social interactions (see [36,37] for references and review). They also share similar mechanisms for processing the type, importance, and value of social information [38\*]. 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 [39]. Cells in the auditory cortex are more responsive to videos of calling monkeys than to auditory or visual signals presented separately [40]. 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 [40]. 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 [10].

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 [38\*]. 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 reward [38\*,41]. 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 [42,43].

Similar neural mechanisms may underlie monkeys’ decisions to vocalize. It is well known, for example, that primates’ control of vocalization during operant conditioning is mediated by activity in the mediofrontal cortex, including the anterior cingulate gyrus [44\*]. More recently, studies of marmosets (*Callithrix jacchus*) have examined the neural mechanisms underlying vocal exchanges between male and female partners [45\*,46\*,47\*]. 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 pre-motor activity occurs in both frontal and auditory cortex [47\*,48\*,49\*]. It appears to be neither sensory-driven nor motor-driven, but instead depends upon the social context, constituting a ‘social monitoring mechanism critical to conversational exchanges’ (47:1036).

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 whistle-plus-high-hoot (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. But 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 sheds 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 [1,2\*,3\*,12]. Like most mammals, however, they 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 [50\*], and we further assume that vocal

communication in contemporary monkeys and apes offers a reasonable approximation to the communication of our pre-linguistic 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 non-linguistic 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 bonds are of paramount importance. Such vocalizations fulfill many of the criteria suggested for language precursors [51]. 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 [2\*,3\*,4\*]. 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 [52,53]. 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

Non-human primates have a relatively small repertoire of calls but use these vocalizations in a highly flexible manner. Like their responses to calls, their use of vocalizations depends upon contextual factors including the listener’s identity, the listener’s recent interactions with the caller and her close associates, and the caller’s judgment of the listener’s likely response. These assessments do not require that callers recognize mental states like

ignorance in others; call usage could easily be shaped through learned contingencies. But 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, before she vocalizes, which of many contextual cues are relevant and which are not. For scientists interested in the evolution of language, vocalizations during social interactions fulfill many of the criteria suggested for language precursors.

## Conflict of interest statement

Nothing declared.

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