

# Function and Intention in the Calls of Non-Human Primates

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**Summary.** Many of the vocalizations produced by non-human primates are functionally semantic, in the sense that they denote objects and events in the external world. Moreover, at least some monkey species appear to assess and compare calls on the basis of their meanings. In their social interactions, non-human primates also use their calls in ways that are functionally analogous to the ways that humans use language. The grunts given by free-ranging baboons, for example, serve to facilitate social interactions and to reconcile opponents following fights. The mental mechanisms underlying the vocalizations of non-human primates, however, appear to be fundamentally different from those that underlie human speech, because monkeys do not apparently call to one another with the intent of modifying or influencing each other's mental states. The alarm and contact calls of monkeys provide information about the signaller's current physical and mental states, but they are not deliberately given to inform or instruct others. Instead, listeners appear to extract relevant information about a call's function based on behavioural contingencies and their own experiences.

## INTRODUCTION

DISCUSSIONS ABOUT THE EVOLUTION OF LANGUAGE typically focus on two apparently fundamental attributes of human speech. The first of these is

semantics, which can be defined loosely as the meaning of words, or sounds. The second is syntax, defined equally loosely as a set of rules for assembling words into meaningful phrases or sentences (Jackendoff 1994; Pinker 1994).

Although the natural communication of monkeys and apes provides few examples of the kind of syntax found in human language (cf. Robinson 1984), there is evidence from a number of monkey species for what might be termed functionally semantic communication. Vervet monkeys (*Cercopithecus aethiops*), for example, use a variety of acoustically different alarm calls to denote predators that hunt in qualitatively different ways (Struhsaker 1967; Seyfarth *et al.* 1980a, 1980b). Each alarm call type elicits a different, apparently adaptive response from monkeys nearby. For instance, alarm calls given to leopards (*Panthera pardus*) cause vervets to run into trees, while alarm calls given to martial and crowned eagles (*Polemaetus bellicosus* and *Stephanoaetus coronatus*) cause vervets to look up or run into bushes. Playback experiments have demonstrated that alarm calls alone, even in the absence of an actual predator, elicit the same responses as do the predators themselves (Seyfarth *et al.* 1980b). The alarm calls, therefore, function as rudimentary semantic signals because each alarm call elicits the same response as would its referent, even when the referent is absent (Hockett 1960; Seyfarth & Cheney 1992).

The alarm calls of vervet monkeys are functionally semantic, but do they qualify as words? To answer this question we must consider not only how signals function in the animals' daily lives but also the proximate causal mechanisms that underlie their production and perception. Since the best studied mammalian communication system is our own, comparison with human language seems a reasonable place to begin.

It is often assumed that animals respond to vocal signals simply on the basis of the calls' physical features, or acoustic properties (e.g. Morton 1977). Humans, by contrast, make judgments about the similarity or difference between words on the basis of an abstraction, their meaning. For example, when asked to compare the words 'treachery' and 'deceit', we typically ignore the fact that the two words have different acoustic properties and describe them as similar because they have similar meanings. 'Treachery' and 'lechery', on the other hand, are judged as different because, despite their acoustic similarity, they mean different things. In making these judgments, we recognize the referential relation between words and the things for which they stand.

The 'ape language' projects provide a number of elegant cases in which chimpanzees (*Pan troglodytes*) have learned to assess and compare signs according to their meaning (e.g. Premack 1976; Matsuzawa 1985; Savage-Rumbaugh 1986). This ability, however, is not restricted to captive apes that have been trained in the use of artificial signs. Vervet monkeys also appear

to have some mental representation of what their vocalizations stand for: when responding to calls, they seem to compare and assess them according to their meanings, and not just their acoustic properties.

When a vervet subject is repeatedly played a tape-recording of another individual's leopard alarm call when there is no leopard in the vicinity, she soon habituates to the call and ceases responding to it. If, however, the subject is then played the same individual's eagle alarm call, she responds strongly to it, in the same way that she would if an eagle had been sighted. Because the two calls have different referents, the subject does not transfer habituation across call types (Cheney & Seyfarth 1988).

Vervets do transfer habituation, however, between call types that have similar meanings. Vervet monkeys are hostile toward the members of neighbouring groups (Cheney 1981). When females encounter another group encroaching on their range, they often utter a loud, long, trilling call (termed a 'wrr'), which seems to function to alert other individuals of the encroachment. Roughly 45% of all inter-group encounters involve only the exchange of wrrs; others, however, escalate into aggressive chases and fights. When groups come together under these more aggressive conditions, females often give an acoustically different 'chutter'. The two calls, wrrs and chutters, therefore, are acoustically different but seem to share the same referent: another group. Moreover, vervets seem to treat the two calls as being, roughly speaking, synonymous. If a subject has habituated to repeated playback of another individual's inter-group wrr, she shows a similarly low level of response when played that individual's inter-group chutter. She transfers habituation from one call type to another, apparently because the two calls have the same general meaning despite their different acoustic properties (Cheney & Seyfarth 1988).

Vervet monkeys, therefore, appear to interpret their calls as sounds that represent, or denote, objects and events in the external world. When one vervet hears another calling, she forms a representation of what the call means. And if, shortly thereafter, she hears a second call, the two calls are compared on the basis of their meaning, and not just their acoustic properties.

## INTENTIONAL COMMUNICATION

The comprehension of words by humans, however, involves more than just a recognition of the referential relation between sounds and the objects or events they denote. As listeners, we interpret words not just as signs for things but also as representations of the speaker's knowledge. We attribute mental states like knowledge and beliefs to others, and we recognize the

causal relation between mental states and behaviour. We are, as a result, acutely sensitive to the relation between words and the mental states that underlie them. If, for example, we detect a mismatch between what another person says and what he thinks, we immediately consider the possibility that he is trying to deceive us.

H. P. Grice (1957) is one of many philosophers who have tried to clarify the distinction between human speech and simpler signalling systems that can nevertheless convey sophisticated, complex information. Grice distinguished the 'non-natural' meaning of linguistic phenomena, in which the speaker intends to modify both the behaviour and beliefs of his audience, from the 'natural' meaning of many other types of signs, in which, for example, thunder and lightning mean that it will soon rain (see also Bennett 1976; Tiles 1987). According to Grice's definition, truly linguistic communication does not occur unless both signaller and recipient take into account each other's states of mind—unless, in other words, both signaller and recipient take what the philosopher Dennett (1987) has called the 'intentional stance'.

All observations and experiments conducted to date suggest that monkeys do not attribute mental states different from their own to other individuals, though the evidence from chimpanzees is more equivocal (reviewed by Cheney & Seyfarth 1990b; Povinelli 1993; van Hooff 1994). Grice's definition of communication, therefore, may be completely irrelevant when applied to most cases of animal communication. Nevertheless, his definition is useful and provocative because it reminds us of precisely what is at stake when we compare non-human primate vocalizations with human language. Perhaps more important, it suggests that there can be communication systems that are complex and even semantic but that do not qualify as language because they fail to meet the criteria of language on intentional grounds.

It is this perspective, which compares a behavioural biologist's focus on function with a philosopher's focus on cognitive mechanisms, that we wish to consider in the remainder of this paper.

### **The social function of primate vocalizations**

Only a small proportion of the vocalizations given by monkeys and apes occur in the form of alarm or inter-group calls. Instead, the most common calls given by many non-human primates are low amplitude grunts, coos, or trills that are given at close range and occur in the context of social interactions or group movement. Many of these calls appear to function to initiate and facilitate social interactions. For example, in Japanese macaques (*Macaca fuscata*), grooming interactions are often initiated

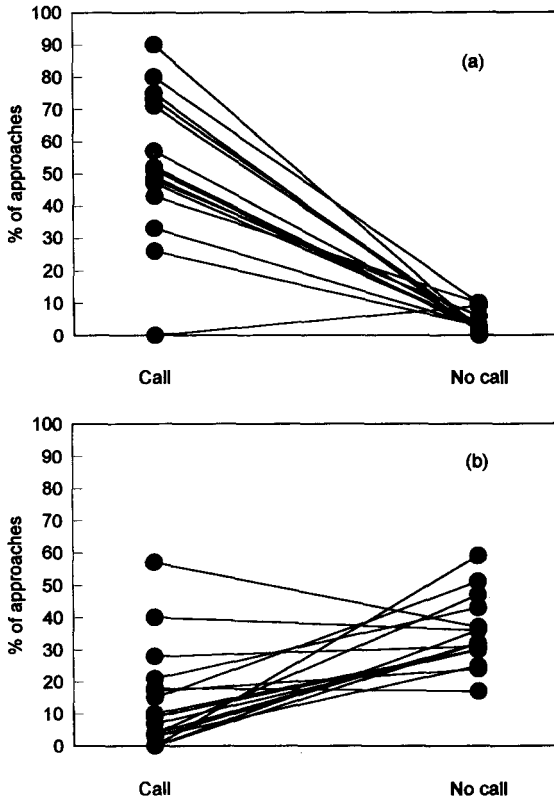
when one female vocalizes to a potential partner (Masataka 1989; Sakuro 1989). Similarly, in stump-tailed macaques (*Macaca arctoides*), individuals that grunt to mothers before attempting to handle their infants are less likely to receive aggression than are individuals that remain silent (Bauers 1993).

From a functional perspective, these calls are interesting because they are in many ways analogous to human speech. Typically, there is no obvious response to the calls from nearby listeners, and it certainly seems as if these vocalizations, like many human conversations, function simply to mediate social interactions and grease the social wheels. Note, however, that it is difficult to describe the function of these calls without adopting an intentional vocabulary on behalf of the signaller. If a call serves to mollify an opponent or a subordinate mother, it seems almost essential that the signaller be able to recognize her partner's anxiety and to signal her own benign intent.

To examine the function of these close-range vocalizations in more detail, we carried out a detailed study of the grunts given by free-ranging female baboons (*Papio cynocephalus ursinus*) in the Okavango Delta, Botswana. Our work focused on an habituated group that included between 19 and 23 adult females (see Cheney *et al.* 1995).

Like adult females in many species of Old World Monkeys, female baboons form stable, linear dominance hierarchies (Seyfarth 1976; Hausfater *et al.* 1982; Smuts & Nicolson 1989). Although most affiliative interactions occur among close kin, adult females also interact with unrelated females, particularly if those females have infants. Normally, if a dominant female approaches a subordinate female, the subordinate is supplanted and moves away. Frequently, however, the dominant female vocalizes to the subordinate, using a low pitched, tonal grunt (Seyfarth, Cheney & Owren, unpublished data). These grunts seem to have an appeasing function, because they increase the probability of a subsequent friendly interaction, such as grooming or infant handling.

We recorded 2,698 incidents in which one female approached another that ranked lower than herself; in 621 (23%) of these cases the dominant female grunted to the subordinate. There were 17 females that could approach at least one lower-ranking, unrelated individual. For 15 of the 17, the mean frequency of approaches to all possible partners that was followed by a friendly interaction was higher if the dominant female first grunted than if she did not (Figure 1a; one-tailed Wilcoxin matched-pairs signed-ranks test, 1 tie,  $t = 1$ ,  $P < 0.001$ ). Similarly, for 14 of 17 individuals the mean frequency with which a female supplanted her lower-ranking partner was higher when she did not call than when she did (Figure 1b;  $t = 10$ ,  $P < 0.001$ ). Results were unaffected by the relative difference in rank



**Figure 1.** The mean proportion of 17 females' approaches toward subordinate partners that was followed by either (a) friendly behaviour by the dominant or (b) a supplant of the subordinate. Approaches are divided according to whether the dominant female grunted as she approached or whether she remained silent.

between the two females. Grunts, therefore, appeared to mediate and facilitate social interactions among unrelated adult females.

If grunts or other vocalizations do function to facilitate affiliative interactions, they might also be expected to play a role in reconciling opponents following aggression. Non-human primates are frequently aggressive toward one another, yet they live in relatively stable, cohesive social groups. Recent studies have suggested that opponents may mollify the effects of aggressive competition by reconciling soon after fighting or threatening one another (e.g. de Waal & van Roosmalen 1979; de Waal & Yoshihara 1983; York & Rowell 1988; Aureli *et al.* 1989; Cheney & Seyfarth 1989; Judge 1991; Aureli 1992; Cords 1992, 1993). Two animals are said to have reconciled if, within minutes of behaving aggressively, they interact in a friendly way by touching, hugging, grooming, or approaching one another.

No study, however, has yet considered the role that vocalizations might play in reconciling former opponents.

Baboon females do sometimes grunt to one another after aggression. In an effort to examine the role of grunts in reconciling opponents, we carried out a number of systematic observations of aggressors and their victims. Whenever two females were involved in an aggressive interaction, we followed the aggressor for 10 minutes to determine whether she subsequently interacted with her victim in any way (Silk, Cheney & Seyfarth, in preparation). In 5% of 502 samples, the aggressor subsequently interacted in a friendly manner with her opponent by touching her, grooming her, or interacting with her infant. Eighty-five per cent of these friendly interactions also included a grunt by the aggressor. In 9% of all cases, the aggressor only grunted to her victim and did not interact with her in any other way.

These observations suggested that vocalizations alone, even in the absence of other affiliative interactions, might function to reconcile opponents. Nevertheless, the significance of the grunts themselves was difficult to assess simply from observations, because grunts often occurred in conjunction with other friendly behaviour, such as grooming or infant handling. To determine whether grunts might function to reconcile opponents even in the absence of other affiliative interactions, therefore, we designed a series of playback experiments (for details of the experimental protocol see Cheney *et al.* 1995).

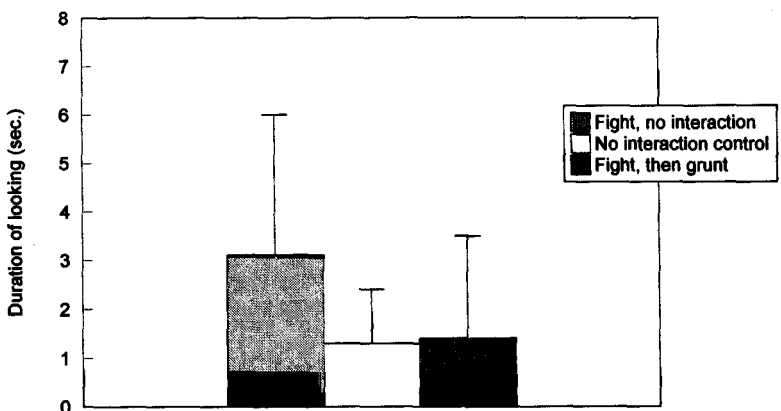
In conducting these experiments, we first waited until a higher-ranking female, A, had threatened or chased an unrelated, lower-ranking female, B. We then followed A for 10 minutes to determine whether she interacted affiliatively with her opponent, and, if so, what form this affiliative interaction took. After this period, but within the next 30 minutes, we played a tape-recording of A's distress scream to B and videotaped B's response. Screams were played back to subjects under three conditions: (1) after A had been aggressive to B and did not interact with her again; (2) after A had been aggressive to B and then grunted to B without interacting with her in any other way; and, (3) after a period of at least 90 minutes in which A and B had not interacted.

We chose screams as playback stimuli because they mimicked a context in which subordinate females are sometimes attacked by dominant individuals. When a female baboon receives aggression from a higher-ranking female or male, she typically screams at her opponent. Frequently, she then 'redirects' aggression by threatening a more subordinate individual. We hypothesized that a subordinate female that heard the scream of an unrelated, higher-ranking individual would interpret this call as a potential threat to herself (see discussion in Cheney *et al.* 1995). We predicted that B would react strongly to the sound of A's scream if A had recently threatened

B but had not reconciled (i.e. grunted) with her. B's response in this context should be stronger than it was following a control period when the two females had not interacted. If, however, A had grunted to B after threatening her, B's anxiety should be diminished. We predicted that B's response after vocal 'reconciliation' would be similar to her response following the control period of no interaction.

There were 15 dyads that met all three test conditions. If a dominant female had grunted to her subordinate opponent following a fight, the opponent responded for a significantly shorter period of time to that female's scream than she did following a fight when no further interaction had taken place (Figure 2; one-tailed Wilcoxon matched-pairs signed-ranks test,  $n = 15$ , 1 tie,  $t = 17.5$ ,  $P < 0.025$ ). Subordinate subjects also responded less strongly to dominant females' screams after a control period of no interaction than after a fight with no reconciliation (Figure 2;  $n = 15$ , 1 tie,  $t = 24$ ,  $P < 0.05$ ). In contrast, subordinate subjects' responses to dominant females' screams following a fight with a vocal 'reconciliation' were statistically indistinguishable from their responses following a control period of no interaction (Figure 2;  $n = 15$ , 2 ties,  $t = 47.5$ , NS).

There were 14 other dyads that met two of the three test conditions described above. For seven dyads, 'fight with no vocal reconciliation' could be compared with the 'no prior interaction' control. For seven other dyads, 'fight with vocal reconciliation' could be compared with the 'no prior interaction' control. Results from these trials further supported the



**Figure 2.** The duration of subjects' responses to the screams of dominant opponents after (1) the dominant threatened the subject and did not interact with her again; (2) the two females had not interacted for at least 90 minutes; and (3) the dominant threatened the subject and then reconciled by grunting to her. Histograms show means and standard deviations for 15 dyads in each of the three conditions. Subjects' responses were scored as looking in the direction of the speaker.



hypothesis that grunts functioned to restore opponents' relationships to baseline levels of tolerance. A significant number of subjects responded more strongly to their opponent's scream after a fight when they had not reconciled than after the control period ( $n = 7$ ,  $t = 1$ ,  $P < 0.01$ ). If, however, the dominant female had grunted to her opponent, the opponent's response was the same as after the control period ( $n = 7$ , 1 tie,  $t = 3.5$ , NS).

Some studies of macaques have suggested that proximity alone may serve a reconciliatory function (de Waal 1989; Cords 1993). And, because baboons typically grunt when in relatively close proximity to one another, it might be argued that proximity, rather than the vocalization, was the reconciliatory mechanism.

In 23% of the 'no reconciliation' fights, dominant opponents approached their victims within the next 10 minutes without vocalizing or interacting with them in any other way. Had proximity alone acted to reconcile opponents, subjects that had simply been approached by their opponents following a fight should have responded as weakly to the playbacks as did subjects that received a grunt. This, however, was not true. Subjects that had only been approached responded significantly more strongly than did subjects that had also received a grunt when they were approached (Mann-Whitney  $U$  test,  $N_1 = 5$ ,  $N_2 = 22$ ,  $U = 22.5$ ,  $P < 0.05$ ).

### **The mechanisms underlying monkeys' calls**

Both observations and experiments suggest that vocalizations constitute a major component of reconciliatory behaviour in female baboons. Even in the absence of more overt friendly behaviour, baboon grunts act to restore the relationships of opponents to baseline tolerance levels. Grunts serve to mediate and repair social relationships. They also function to initiate and facilitate affiliative contact between individuals of disparate ranks that might not otherwise interact.

What, however, are the mechanisms underlying apparently reconciliatory grunts? Do dominant females give grunts with the intent of appeasing their former victims? One explanation for the prevalence of vocalizations following conflicts is that dominant females grunt in order to alleviate their opponent's anxiety and to reassure them that they are no longer angry. An equally plausible explanation, however, is that dominant females simply grunt to their victims because they are in a friendly mood and wish to interact with their opponents' infants.

Although these two explanations are functionally equivalent, they are based on quite different underlying mental mechanisms. The first explanation focuses on the signaller, and assumes that calling individuals attribute

mental states different from their own to their audience. The second focuses on the audience, and assumes that listeners respond to calls on the basis of behavioural contingencies. This latter explanation requires that subordinate females learn, through experience, that grunts signal a low probability of attack; as a result, their anxiety is diminished when a dominant female grunts to them.

Despite their functional equivalence, the distinction between these two explanations is crucially important to any discussion concerned with the evolution of language. If, as Grice and others have argued, true linguistic communication cannot occur unless both speaker and listener take into account each other's states of mind, then monkeys cannot be said to communicate unless they use calls like reconciliatory grunts with the intent of influencing each others' beliefs and emotions. By contrast, if monkeys are incapable of recognizing the relationship between what an individual says and what she thinks, a call that functions to reconcile an opponent will be based on fundamentally different underlying mental mechanisms than reconciliation in the human sense of the term, in which individuals deliberately act to appease or overcome the distrust or animosity of another.

In fact, there is very little evidence that monkeys or other animals ever take into account their audience's mental states when calling to one another. Consider alarm calls, for example. The alarm calls of many birds and mammals are not obligatory, but depend on social context. Individuals often fail to give alarm calls when there is no functional advantage to be gained by alerting others; for instance, when they are alone or in the presence of unrelated individuals (e.g. ground squirrels, Sherman 1977; downy woodpeckers, Sullivan 1985; vervet monkeys, Cheney & Seyfarth 1985; roosters, Gyger *et al.* 1986). However, while this 'audience effect' clearly requires that a signaller monitor the presence and behaviour of group companions, it does not demand that he also distinguish between ignorance and knowledge on the part of his audience. Indeed, in all species studied thus far, signallers call regardless of whether or not their audience is already aware of danger. Vervet monkeys, for example, will continue to give alarm calls long after everyone in their group has seen the predator and retreated to safety.

Experiments with captive rhesus (*Macaca mulatta*) and Japanese macaques have demonstrated that mothers do not alter their alarm calling behaviour depending upon the mental states of their offspring. When given the opportunity to alert ignorant offspring of potential danger, they do not change their alarm calling behaviour (Cheney & Seyfarth 1990a). Similarly, if vervet monkeys attributed mental states different from their own to others, they might be expected to correct or instruct their offspring in the appropriate use of alarm calls. This they never do. Infant vervets give eagle alarm calls to many bird species, like pigeons, that pose no danger to them.

Adults, however, never correct their offspring when they make inappropriate alarm calls, nor do they selectively reinforce them when they give alarm calls to real predators, like martial eagles. Instead, infant vervets seem to learn appropriate usage simply by observing adults (Seyfarth & Cheney 1986).

In summary, there is no doubt that the alarm calls given by monkeys function to inform nearby listeners of quite specific sorts of danger. They seem, however, simply to mirror the intent and state of the signaller, and they fail to take into account their audience's mental states.

A similar disregard for one's audience's mental states seems to characterize the contact and food calls given by many species of animals. Despite numerous attempts to test the hypothesis that foraging animals share information about the location of food or each other's relative positions in the group progression, no study has yet been able to demonstrate that individuals deliberately inform one another. For example, although carrion birds and bats that feed on widely dispersed food sources could potentially share information at common roosting sites, individuals appear to locate food either by following others or simply by finding it themselves (e.g. crows: Richner & Marclay 1991; turkey vultures: Prior & Weatherhead 1991; bats: Wilkinson 1992; red kites: Hiraldo *et al.* 1993).

Even in the case of non-human primates, evidence for intentional information sharing is lacking. Although listeners can potentially use calls to maintain contact with signallers or to locate food resources, the proximate cause of the calls appears to be the current state or status of the signaller. There is no indication that signallers selectively answer the calls of separated individuals, or that they call more upon discovering a new food source than upon returning to a tree that was recently visited by many group members. For example, capuchins (*Cebus capucinus*) and squirrel monkeys (*Saimiri sciureus*) give progression calls primarily when they themselves are moving or about to move (Boinski 1991, 1993). Spider monkeys (*Ateles geoffroyi*) call when they arrive at a fruiting tree, but the calls only function to recruit other subgroups a small proportion of the time (Chapman & Levebre 1990). Similarly, although chimpanzees often give pant hoots upon arrival at large unoccupied fruiting trees, parties that call are not joined more than parties that remain silent (Clark & Wrangham 1994), nor are individuals that remain silent punished for failing to alert others (but see Hauser & Marler 1993 for a possible exception in rhesus macaques). These observations have forced some revision of the hypothesis that calls such as chimpanzees' pant hoots function to alert others to food (Wrangham 1977). Indeed, current evidence suggests that the calls may instead function to signal the caller's status (Mitani & Nishida 1993; Clark & Wrangham 1994).

### Baboon contact barks

When moving through wooded areas, female and juvenile baboons often give loud barks that can be heard up to 500 metres away (see also Byrne 1981). These 'contact barks' can potentially function to maintain group cohesion because, upon hearing one or more barks, an individual that has lost contact with others knows immediately where at least some group members are.

Because contact barks are often temporally clumped, with many individuals giving calls at roughly the same time, baboons often appear to be answering one another. What is not clear, however, is whether baboons give such calls with the intent of maintaining contact with each other, or whether the calls simply reflect the signaller's own circumstances (i.e. separated from the group). Hypotheses based on mental state attribution predict that individuals will answer the contact barks of others even when they themselves are in the centre of the group progression and at no risk of becoming separated from others. If, however, baboons are incapable of understanding that other individuals' mental states can be different from their own, they should be unable to recognize when another individual has become separated from the group unless they themselves are also peripheral and at risk of becoming separated. Under these circumstances, contact barks will simply reflect the state and location of the signaller.

To test between these two hypotheses, we gathered data on the social context of the contact barks given by 23 adult females over a three month period. Analysis of almost 2000 individually identifiable barks revealed a highly significant clumping of calls. Indeed, 92% of the calls given by females occurred in the five minutes following a previous call from either another female, the caller herself, or both (see Cheney *et al.* 1996, for details of the sampling protocol).

If females had given 'answering' calls at random, then 96% (22/23) of each individual's calls should have followed a call by another female, and 4% (1/23) should have occurred following one of her own calls. In fact, the mean proportion of 'answering' calls that followed a call by another female was 74%. Twenty-two of the 23 females gave fewer contact barks in the five minutes following a contact bark by another female than would have been expected by chance (two-tailed binomial test,  $P < 0.001$ ). Even close kin failed to answer each other's contact barks more often than expected by chance.

In contrast, the mean proportion of contact barks given by females that followed one of their own contact barks was 66%. All 23 females 'answered' themselves at least 10 times more than expected by chance ( $P < 0.001$ ).

These data argue against the hypothesis that calls were clumped in time because females were answering one another. Instead, it seems that clumping of calls occurred primarily because each female herself, when she called, was likely to give a number of calls one after the other.

As a further test of the hypothesis that females did not answer the contact barks of other females, but instead gave barks depending primarily on their own position, we carried out a series of 36 playback experiments, in which we played to subjects the contact bark of a close female relative (either a mother, daughter, or sister) (Cheney *et al.* 1996).

In 19% of trials, subjects did in fact 'answer' their relative's contact bark by giving at least one bark themselves within the next five minutes. (In one additional experiment the subject called in the seventh minute after the playback.) In no case did other, unrelated females in the vicinity respond to the playbacks with a call.

At first inspection, these results might be taken as weak evidence for the selective exchanging of contact barks among close kin. Closer examination, however, reveals that subjects 'answered' playbacks of their relatives' barks primarily when they themselves were peripheral and at risk of becoming separated from the group. Subjects that were in the last third of the group progression were significantly more likely to answer their relatives' contact barks than were subjects that were in the first two thirds (Figure 3;  $X^2 = 4.43$ ,  $P < 0.05$ ). Similarly, they were significantly more likely to give answering barks when there was no other female within 25 metres than if there was at least one other female nearby (Figure 3;  $X^2 = 5.86$ ,  $P < 0.05$ ).

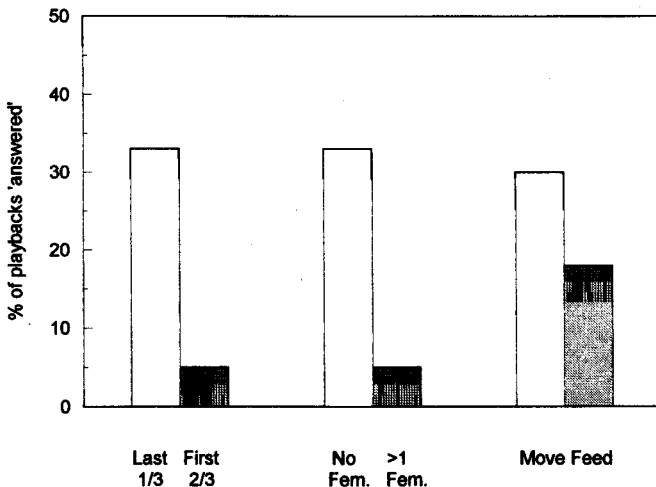


Figure 3. The context in which subjects 'answered' their relatives' contact barks in the 5 minutes following playback. Data are based on 36 trials involving 18 subjects.

Subjects were also more likely to call when the group was moving rather than feeding, though not significantly so.

Both observations and experiments suggest, therefore, that baboons do not give contact barks with the intent of sharing information, even though the calls may ultimately function to allow widely separated individuals to maintain contact with one another. Like the progression, contact, and food calls given by other species of primates, baboon contact barks appear to reflect the signaller's own state and position rather than the state and position of others.

## DISCUSSION

The vocalizations of non-human primates share a number of similarities with human speech. Many of the calls given by vervet monkeys, for example, are functionally semantic and serve to denote objects or events in the external world. Vervets seem to compare and classify calls according to their meaning, and not just their acoustic properties. They judge some acoustically different calls to be the same when the calls refer to similar events. The monkeys behave, in other words, as if they recognize the referential relation between calls and the things for which they stand.

The calls given by monkeys during social interactions also appear to serve many of the same purposes as human speech, in the sense that they act to mediate social interactions, to appease, and to reconcile. Other calls function to inform individuals about the caller's location and to maintain group contact and cohesion.

Despite these functional similarities, however, the mental mechanisms underlying non-human primate vocalizations appear to be fundamentally different from the mechanisms underlying adult human speech. When calling to one another, monkeys seem to lack one of the essential requirements of human speech: the ability to take into account their audience's mental states.

Explanations based on mental state attribution make quite specific predictions about the pattern and context of calls. A vervet or macaque that attributes mental states different from her own to others should adjust her alarm or inter-group calls according to her audience's knowledge, and she should selectively inform ignorant individuals more than knowledgeable ones. She should also correct her offspring when it gives alarm calls to inappropriate species. A dominant female baboon that attributes emotions to others should grunt to a subordinate victim in order to alleviate her

victim's anxiety even though, being dominant, she feels no anxiety herself. Similarly, a baboon capable of attributing confusion or anxiety to others should answer other individuals' contact barks regardless of her own position in the group progression.

Despite a variety of tests, however, there is no evidence that monkeys attribute mental states to one another. Monkeys appear not to call with the intent of providing information or influencing listeners' beliefs. Instead, listeners appear to respond to calls based on learned behavioural contingencies.

Although vervet monkeys, like many other species of birds and mammals, may vary their rates of alarm calling depending upon the composition of their audience, they do not act deliberately to inform ignorant individuals more than knowledgeable ones (Cheney & Seyfarth 1990a, 1990b). A vervet's alarm call alerts other animals regardless of whether or not they are already aware of the danger. In a like manner, infant vervets are not explicitly instructed to respond to some prey species rather than others. Instead, they learn to recognize their predators by observing the behaviour of adults (Seyfarth & Cheney 1986).

In the case of baboons' reconciliatory grunts, it seems likely that dominant females grunt to their former victims because they wish to interact in a friendly way with them, usually because these individuals have young infants (Cheney *et al.* 1995; Silk, Cheney, & Seyfarth, in preparation). Through past experience, and perhaps also by observing the interactions of others, the victims learn that grunts honestly signal a low probability of aggression. They therefore relax when their former opponents approach.

Similarly, baboons give contact barks when they are at the group's periphery and at risk of becoming separated from others. Through experience, listeners learn that they can maintain contact with at least a subset of the group simply by listening to other individuals' calls.

In all cases, listeners are able to extract relevant information about a call's function based on their own experiences. Their responses need not take into account the signaller's mental states at all. Indeed, in each case, the meaning and function of the calls are to a large part determined by the listener rather than the signaller. Upon hearing a vervet's inter-group wrr, the listener deduces that another group is nearby, and this representation allows her to ignore any subsequent inter-group vocalizations, even those with different acoustic properties. Upon hearing a dominant baboon's grunt, the subordinate listener deduces that she will not be attacked. Upon hearing another baboon's contact bark, the listener deduces the group's location and direction of travel. In each case, the listener extracts rich, semantic information from a signaller who may not, in the human sense, have intended to provide it.

From the listener's perspective, then, non-human primate vocalizations share many similarities with human semantic signals. Not only do calls function to inform others of specific features of the environment and the signaller's emotions and intentions, but they also appear to be judged and classified according to the representations which they instantiate in the listener's mind.

From the signaller's perspective, however, there are striking discontinuities between non-human primate vocalizations and human language, at least as it manifested in adults. These discontinuities are based not so much on the formal properties of the calls themselves than on the mental mechanisms underlying call production. In marked contrast to adult human language, the calls of monkeys do not seem to take into account listeners' mental states. As a result, monkeys cannot communicate with the intent of appeasing those who are anxious or informing those who are ignorant.

There is no doubt that the vocal communication of non-human primates mediates complex social relationships and results in the transfer of quite specific sorts of information. Equally clearly, non-human primate vocalizations affect listeners' mental states, in the sense that they change what other individuals know about the world and affect what they are likely to do. Compared with human language, however, the vocalizations of monkeys achieve this end almost by accident, without individuals being aware of the features of the system in which they are participating. Monkeys, and perhaps also apes, are skilled at monitoring each other's behaviour. There is little evidence, however, that they are equally adept at monitoring each other's states of mind. A challenge for the future will be to identify the selective factors that might have favoured the evolution of mental state attribution in the language and behaviour of our early ancestors.

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