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Behavioral mechanisms underlying vocal communication in nonhuman primates

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In the wild, nonhuman primate vocalizations signal the presence of different predators, provide information about the group's location and movement, facilitate friendly interactions, and lead to reconciliation between individuals who have recently exchanged aggression. Current research examines the mechanisms that underlie such communication. Playback experiments demonstrate that subjects treat vocalizations as semantic signals, in the sense that they compare signals according to their referents and not just their acoustic properties. Results provide no evidence, however, that subjects recognize one another's mental states. Calls that provide information about the group's location or movement are given by baboons only when they themselves are lost; individuals at the group's center apparently do not call to inform peripheral animals of their location. Calls that lead to reconciliation are best explained by assuming that callers and recipients have learned, through experience, that a vocalization is rarely followed by aggression and often followed by friendly behavior. The inability of animals to recognize what other individuals know, believe, or desire constitutes a fundamental difference between nonhuman primate vocal communication and human language.

It has become almost axiomatic to assert that the vocalizations of nonhuman primates differ fundamentally from the speech of humans. The truth of this assertion, however, depends largely on whether or not one defines language exclusively in terms of its syntactic properties. For while it is true that there is little evidence for syntax in the calls of monkeys and apes, research has also shown that certain nonhuman primate vocalizations are semantic, in the sense that they designate or refer to objects or events external to the signaler (see reviews by Cheney & Seyfarth, 1990b; Hauser, 1996).

Discussions of the semantic content of primate vocalizations have generally assumed a functional stance, and focused on the responses that calls evoke in listeners rather than on the mental processes underlying call production. This approach is taken largely out of methodological necessity, because we can measure an animal's responses to calls but not the mental processes that underlie them. The current emphasis on function, however, also reflects a deeper analytical problem that has vexed philosophers for several millennia: what does it mean to say that one stimulus "means" something to an organism?

Even in the well-studied case of human language, it has proved extremely difficult to identify the sorts of concepts and mental representations that underlie a speaker's words. When a human (or a monkey) shouts "Leopard!" upon sighting a leopard, does the word (or alarm call) map directly onto a mental concept? If so, is the concept "leopard" a complete, innate depiction of a large, yellow, spotted cat, or is it built up from several more basic concepts, such as "yellow," "spotted," and "cat"? Or is the word (or alarm call) more accurately described as a propositional attitude (see, e.g., Fodor, 1987) that incorporates information both about the object itself and about the speaker's disposition to behave in a certain way toward that object?

It is equally difficult to specify precisely how a speaker's word maps onto the concepts and mental representations of his audience. When one individual warns another of a leopard's approach, how can we ascertain whether the two individuals have the same mental concept of "leopard"? And if each individual's concept of a leopard is to some extent unique (as it must inevitably be), how can communication ever occur? The logical impossibility of ever establishing whether the meaning of a word to one person is precisely the same as the meaning of that word to another has prompted some philosophers to argue that the full semantic content of words can never be known. Although this is undoubtedly true, such extreme solipsism is, at least for a functional analysis of language, irrelevant. Speech is first and foremost a social behavior, and humans do, at least implicitly, arrive at an operational agreement about word meaning. If they did not, social interactions would be impossible.

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The problem of determining the "meaning" of a signal to both the signaler and his audience becomes even more fraught with methodological complexities when we turn to other species, whose members we cannot even interview. Smith (1965, 1977) was perhaps the first ethologist to address this problem directly. He emphasized that signals must be analyzed from two different perspectives, that of the signaler and that of the recipient. Distinguishing between signaler and recipient is important, because in many cases the information made available to a listener is quite different from the information that the signaler intends to convey. Indeed, in many cases the "meaning" that a listener extracts from a signal may have very little to do with the information that the signaler "intended" to transmit. A human infant's cry may be completely involuntary but it nonetheless provides adults with very specific information. A frog's croak provides information to nearby females about the caller's suitability as a mate (Rand & Ryan, 1981), to nearby males about the location of a competitor (Ryan, 1985), and, despite the croak's ventriloqual properties, to nearby bats about the caller's location (Ryan, Tuttle, & Rand, 1982). The mechanisms that cause the caller to croak in the first place are entirely different. Nevertheless, the call functions to communicate quite specific information, to which conspecifics respond appropriately.

Because monkeys and other nonhuman species cannot be asked what sort of information they intend to convey when they utter a call, inferences about the meaning, function, and even the mental processes underlying the production of vocalizations have typically been obtained indirectly, by observing the responses that the calls evoke in others. However, because the meaning of a call to the signaler may be quite different from the meaning of the call to the listener, this method is far from satisfactory. Few studies have pointed out this distinction.

There is yet another problem. Even though the vocal signals of at least some nonhuman species seem to function as words do, there is still considerable doubt about whether such signals are truly communicative in a linguistic sense. The comprehension of words by humans involves more than just a recognition of the referential relation between sounds and the objects or events that 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 such as knowledge and beliefs to others, and we recognize the causal relation between mental states and behavior. We are, as a result, acutely sensitive to the relation between words and the mental states that underlie them. For example, if 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.

Grice (1957) is one of many philosophers who have tried to clarify the distinction between human speech and simpler signaling systems that can nevertheless convey complex information. Grice distinguished the "nonnatural" meaning of linguistic phenomena, in which the speaker intends to modify both the behavior 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 signaler and recipient take into account each other's states of mind.

All observations and experiments conducted to date suggest that monkeys do not attribute mental states different from their own to other individuals (reviewed by Cheney & Seyfarth, 1990a; Povinelli & Eddy, 1996c). 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 animal 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. By framing questions about communication in terms of, among other things, the presence or absence of mental state attribution, we focus attention on the different roles of signaler and recipient, and on the differences between a signal's functions and the mechanisms that give rise to it. We also highlight a property of communication that, in the future, will likely be regarded as constituting one of the fundamental differences between animal communication and human language.

Below, we describe some recent attempts to investigate the semantic features of nonhuman primate vocalizations and the mental processes that underlie them. After briefly discussing our field methods and the logic underlying our playback experiments, we review data on the antipredator alarm calls of vervet and diana monkeys. Results demonstrate that these vocalizations function to inform others about the identity of nearby predators; however, these experiments reveal little about the behavioral mechanisms underlying this transfer of information. To explore this issue further, we review the results of habituation/dishabituation experiments in which subjects were asked to make same/different judgments about vocalizations and reveal the criteria used in making their assessment. Results demonstrate that monkeys compare vocalizations according to their referents, not just their acoustic properties. The animals' behavior can be explained by an associative account, but only if we assume that the associations formed between an external stimulus and a mental representation include, as part of the representation, some kind of image of the event and information about the individual who is vocalizing.

We then turn to a variety of experiments designed to examine how vocalizations function in social interactions and whether the representations of call meaning include—in addition to information about external referent and caller identity—information about the caller's mental state. In tests involving captive macaques, mothers were given information about food or predators that their offspring did not possess. The mothers' behavior gave no indication that they recognized their offsprings' ignorance. In a study of the "contact barks" given by free-ranging baboons, adult females heard the calls of other individuals who were separated from the center of the group. They answered such calls only if they themselves were also peripheral or separated, suggesting that they cannot recognize the mental state of a signaler when it is different from their own. Finally, in studies of the most common vocalization used by baboons—a grunt—we show that grunts function to appease and to reconcile, but they achieve this end without any recognition, on the part of either caller or recipient, of the other animal's mental state. In the General Discussion, we consider the extent to which results are consistent with an associative account of primate vocal communication, and we discuss the different constraints acting on the signaler and recipient in any communicative event.

GENERAL METHODS

Field playback experiments allow a human observer to present the calls of specific individuals to subjects under a variety of different conditions. When combined with behavioral observations of known individuals, they can reveal information not only about the content of the calls themselves but also about how the calls function in social interactions.

Calls chosen as playback stimuli are tape-recorded from known individuals living in the group at the time. When first recorded, the context of the call is noted in as much detail as possible, including, for example, the behavior of the signaler, the behavior and identities of other individuals within a specified radius, and the proximity of predators or neighboring groups. In recent years, it has become possible to create playback tapes with the use of computer software, thus ensuring that the calls chosen as stimuli have the desired acoustic structure and are free of background noise.

When they are played predator alarm calls or calls associated with territorial defense, monkeys often respond in qualitatively different ways—for example, by running into trees or approaching the speaker (e.g., Mitani, 1985; Robinson, 1981; Seyfarth, Cheney, & Marler, 1980; Waser, 1977). In these cases, data on responses can be used to make inferences about the information conveyed by a vocalization. Calls associated with social interactions, however, typically evoke either no response at all or a simple orientation toward the speaker (e.g., vervet monkey screams, grunts, and intergroup calls, Cheney & Seyfarth, 1980, 1982a, 1988, and Hauser, 1986; rhesus macaque screams, S. Gouzoules, H. Gouzoules, & Marler, 1984; see below). Although these reactions are the same as those evoked by naturally occurring intragroup vocalizations (and thus lead us to conclude that our playbacks have accurately mimicked natural behavior), the lack of qualitatively distinct responses complicates the interpretation of call meaning. If we expect that looking toward the speaker will be the only response elicited by a playback experiment, we design matched pairs of trials, alike in all but one respect, and then compare subjects' response durations under two different conditions. A consistent difference in the duration of looking allows us to make inferences about the different sorts of information conveyed by different calls, or by the same call under different circumstances.

Finally, in some trials, subjects show no immediate response to playback of a call but their subsequent behavior is nonetheless affected. Having heard a particular call from individual X, for example, a subject may be more likely to approach X in the next 30 min than if no call had occurred or if a different individual's call had been played. Such long-term changes in behavior allow us to draw conclusions about the information conveyed to particular individuals by different vocalizations.

Many of the playback experiments described below assume that monkeys can distinguish among the calls of different individuals. Evidence for individual recognition by voice in nonhuman primates is now widespread (e.g., vervet monkeys [*Cercopithecus aethiops*], Cheney & Seyfarth, 1980, 1982a, 1982b, 1988; rhesus macaques [*Macaca mulatta*], S. Gouzoules et al., 1984, Hansen, 1976, and Rendall, Rodman, & Emond, 1996; pigtail macaques [*Macaca nemestrina*], H. Gouzoules & S. Gouzoules, 1989; mangabeys [*Cercocebus albigena*], Waser, 1977; squirrel monkeys [*Saimiri sciureus*], Kaplan, Winship-Ball, & Sim, 1978; titi monkeys [*Callicebus moloch*], Robinson, 1981; gibbons [*Hylobates muelleri*], Mitani, 1985).

THE PREDATOR ALARM CALLS OF VERVET AND DIANA MONKEYS

At least some of the calls produced by nonhuman primates appear to designate referents external to the signaler. For example, certain Old World monkeys (and probably many other birds and mammals; see Cheney & Seyfarth, 1990b) produce acoustically different alarm calls when they encounter different predators, and each alarm call type elicits a different, adaptive response from those nearby. The same monkeys also give acoustically distinct calls when they encounter neighboring groups of conspecifics. What can be said about the mechanisms that underlie call production and response, or the nature of the information conveyed by these vocalizations? Does either the caller or the recipient recognize the referential relation that exists between a call and the thing for which it stands? Does either recognize that a call provides information not only about an external referent but also about the caller's knowledge about that referent?

Experiment 1

In the open savanna woodlands of East Africa, vervet monkeys give acoustically different alarm calls in response to different classes of predators. Each alarm call type elicits a different, apparently adaptive escape response from other vervets nearby (Struhsaker, 1967). These responses can be elicited by playback experiments conducted in the absence of an actual predator. For example, when animals foraging on the ground are played a "leopard alarm call" previously tape-recorded from a member of their group, they run into trees, where they are safe from a leopard's attack. In contrast, when subjects are played an "eagle alarm call" they typically look up in the air or run into bushes, the only safe refuge from an eagle. When played a "snake alarm call," they stand on their hind legs and peer into the grass around them (Seyfarth et al., 1980).

Two additional observations provide insights into the mechanisms that underlie alarm call production. First, infant vervets do not begin to give alarm calls until they are 3–4 months old. When they do, they make frequent "mistakes," and give alarm calls to species such as warthogs, small hawks, or pigeons that pose no danger to them. Their mistakes, however, are not entirely random: infants give leopard alarm calls almost exclusively to terrestrial mammals and eagle alarm calls only to birds and objects in the air. Infant vervets thus appear to begin alarm-calling with a strong predisposition to divide the species that they encounter into broad, qualitatively different categories. With age and experience, they sharpen the relation between a particular alarm call type and a specific external referent (Seyfarth & Cheney, 1986, 1997).

Even when the appropriate stimulus is present, however, the production of an alarm call is not an obligatory reflex: vervets can either produce or withhold alarm calls, depending upon the circumstances. Adult females, for example, give alarm calls at significantly higher rates when accompanied by their kin than when accompanied by an unrelated juvenile (Cheney & Seyfarth, 1985), and lone animals attacked by a predator often remain silent (Cheney & Seyfarth, 1990b).

Discussion

Vervet monkey alarm calls function as rudimentary semantic signals, because each call type elicits the same response as its putative referent, even when the referent is absent (Cheney & Seyfarth, 1990b; Seyfarth & Cheney, 1992). When one vervet hears another give an eagle alarm call, the listener responds as if he has seen the eagle himself. This suggests that in the listener's mind the call stands for, or conjures up images of, an avian predator even if the bird itself cannot be seen.

But of course this conclusion could also be mistaken. Playback experiments help to clarify how vocalizations function in the daily lives of animals, but they reveal little about the mechanisms that underlie call production and/or perception. Although vervet alarm calls function in a rudimentary semantic manner, from the data presented thus far we cannot determine whether vervets recognize the referential relation that exists between their calls and features of the environment, nor can we establish whether vervets, in responding to another animal's alarm call, interpret this vocalization as a representation of the caller's knowledge. Subsequent experiments have explored these issues in greater detail.

Experiment 2

Arboreal diana monkeys (*Cercopithecus diana diana*) in the dense, primary rainforest of the Ivory Coast are preyed upon by four different predators that use two distinct hunting methods. The first method, *pursuit*, is employed by chimpanzees and human hunters; these predators continue to pursue their prey even after their presence has been detected. The second method, *surprise*, is employed by leopards and crowned eagles that depend on sudden, unanticipated attacks.

When diana monkeys are played tape-recordings of the vocalizations of pursuit hunters, they fall silent and move quietly to the upper reaches of the forest canopy. In contrast, when the same monkeys are played the vocalizations of surprise predators, they respond with a cacophony of loud alarm calls. The alarm calls given to leopards, or to playback of leopard vocalizations, are acoustically different from those given to eagles or to playback of eagle vocalizations. In addition, the alarm calls given by males to each of these predators are acoustically different from the corresponding alarm calls given by females (Figure 1; Zuberbühler, Noe, & Seyfarth, 1997).

Apparently, diana monkey alarm calls have evolved as the result of two selective pressures. First, like those of vervet monkeys, the alarm calls of diana monkeys convey information to conspecifics about the presence of a particular type of predator. Second, the calls also convey to surprise hunters the fact that they have been sighted (Zuberbühler et al., 1997). Anecdotal observations indicate that, once they have heard alarm calls from diana monkeys, surprise hunters like leopards and crowned eagles leave the area. They act as if they realize that further hunting attempts are unlikely to succeed (Zuberbühler, personal observation). By contrast, predators that rely on pursuit are actually helped by loud noises from the monkeys. Human hunters report that diana monkeys are much more difficult to shoot if they remain silent.

Experiment 3

To test the hypothesis that the calls given by diana monkeys in response to leopards and eagles designate different predators, Zuberbühler et al. (1997) used as playback stimuli the leopard and eagle alarm calls given by adult males. The males' different alarm calls were played to groups of females, who responded by giving choruses of their own predator-specific alarm call types. When played a male's leopard alarm call, females responded by giving the same type of alarm call that they gave in response to playbacks of a leopard's growl. In contrast, when they were played a male's eagle alarm call, females responded with the same type of call that they gave in response to playbacks of a crowned eagle's shriek (Zuberbühler et al., 1997).

Discussion

The most striking difference between these experiments and those conducted with vervet monkeys is that playbacks of diana monkey alarm calls elicited vocal responses, whereas playbacks of vervet alarm calls did not. As a result, the diana monkey experiments permit a more accurate assessment of the mechanisms that underlie call production.

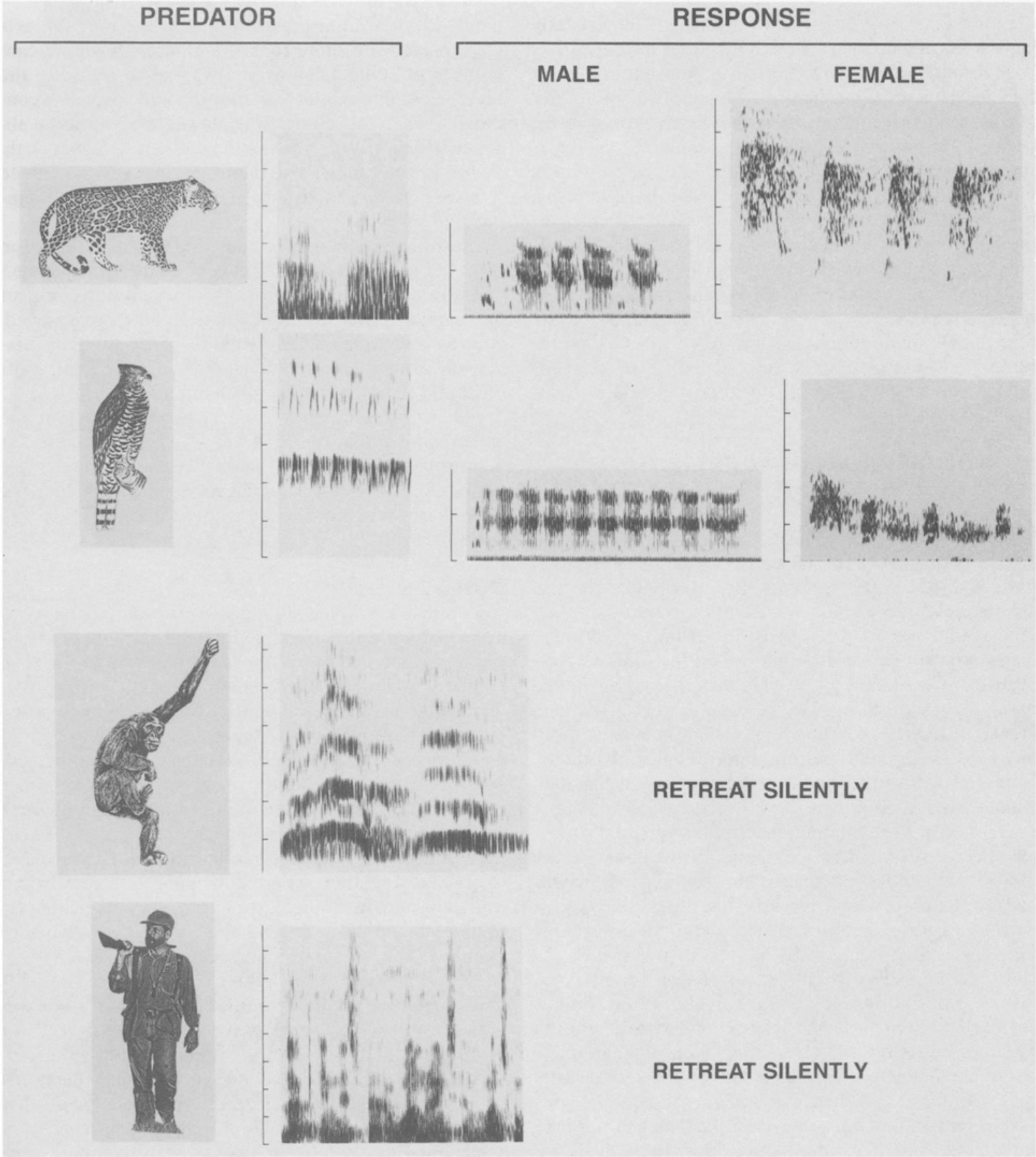

Figure 1. The predator species that prey on diana monkeys, their calls, and the responses of diana monkeys to them. Predators are depicted on the left, along with sonograms of their calls that were played to diana monkeys. On each sonogram, the x-axis indicates time (the duration of the chimpanzee's call is 1.75 sec) and the y-axis indicates frequency (in units of 1 kHz). Diana monkey responses, including the alarm calls given by adult males and adult females, are depicted on the right.

When a female diana monkey hears a male give his version of a leopard alarm call, she produces her own, acoustically different, version of a leopard alarm call. Acoustically, this call is the same as the call that she produces when she hears a leopard's growl. Similarly, when a female diana monkey hears a male give his eagle alarm call, she produces her own version of an eagle alarm call. This call is acoustically different from the male's eagle alarm but similar to the call that the female gives when she hears the shriek of a crowned eagle.

In producing their different alarm calls, therefore, female diana monkeys do not copy the sounds made by predators or by diana monkey males, but instead translate the information contained in these calls into the production of their own acoustically distinct yet semantically similar vocalizations. Although by no means definitive, such results are difficult to explain without assuming that females have some mechanism—associative or not—for (1) deducing information about the presence of different predators from different auditory stimuli, (2) recognizing that two auditorily distinct calls, like the growl of a leopard and the leopard alarm of a male diana monkey, nonetheless indicate the presence of the same kind of predator, and (3) "translating" the information thus obtained into an alarm call of their own, which is itself acoustically different from these other vocalizations. The latter observation raises the strong possibility that, in the mind of a female diana monkey, some sort of mental representation of a leopard or an eagle serves as an intervening variable between hearing one type of sound and producing another.

THE INTERGROUP VOCALIZATIONS OF VERVET MONKEYS

When does a monkey's call cease to become a sound and become a word? This happens, David Premack (1976) has suggested, when the properties ascribed to the call are not those of a sound but those of the object that it denotes. When comparing words, for example, we judge them to be similar or different not on the basis of their acoustic properties (e.g., whether they rhyme) but on the basis of their meaning. Do the calls of vervet or diana monkeys qualify as "words" in this stronger sense? Do monkeys understand the referential relation that holds between vocalizations and the objects or events that they denote?

We used a habituation/dishabituation method to test whether vervet monkeys compare vocalizations on the basis of their acoustic properties or their apparent meaning. The stimuli were two calls that the monkeys give during territorial encounters with neighboring groups. The first, a long, loud, trill (the *wrr*) is given when another group has first been spotted. It seems to alert the members of both groups that a neighboring group has been seen (Cheney, 1981). The second vocalization, a harsh, raspy sound (the *chutter*) is given when an intergroup encounter has escalated into aggressive threats, chases, or fighting. When analyzed acoustically, the wrrs of different individuals are more alike than any wrr is to any chutter, and the chutters of different individuals are more alike than any chutter is to any wrr. Within each class of vocalizations, however, the calls of different individuals are clearly distinguishable statistically (Cheney & Seyfarth, 1988). In sum, wrrs and chutters are acoustically different classes of calls that have broadly similar referents. Both provide information about the proximity of another group.

To determine whether vervets recognize the referential similarity between wrrs and chutters, we repeatedly played a given female's wrr to subjects at 20-min intervals. Because no other group was present at the time that playbacks were conducted, subjects rapidly habituated to the call. After eight presentations of the wrr, subjects were played the same female's chutter. A significant number of subjects showed a weaker response to the playback of this chutter than they did under baseline conditions, when the chutter was played to them in the absence of prior wrr vocalizations (Cheney & Seyfarth, 1988). Results suggested, therefore, that vervets judged wrrs and chutters to be similar on the basis of their similar referential properties.

Interestingly, however, the transfer of habituation from wrr to chutter occurred only when the same female's calls were played. If, following repeated playbacks of one female's wrr, a different female's chutter was played, subjects showed an increment in response strength. Vervets, therefore, appeared to take note of both a call's referent and signaler identity when attending to calls.

Subjects also failed to transfer habituation from one call to another if the two calls had different referents. After habituating to repeated playbacks of a given female's eagle alarm call, for example, subjects nonetheless attended strongly to the same female's leopard alarm call (Cheney & Seyfarth, 1988).

Discussion

Compared with the studies of vervet and diana monkey alarm calls, these tests address the question of meaning and reference more directly, by asking animals to compare two vocalizations and to reveal the criteria that they use in making their comparison. By one hypothesis, our results are best explained as a form of sensory preconditioning (e.g., Brogden, 1939; Jacobson & Premack, 1970) in which two stimuli are judged to be similar because of prior temporal juxtaposition. Intergroup wrrs and chutters, for example, might have been judged as similar not because they have similar referents but because they occur together, whereas leopard alarm calls and eagle alarm calls do not. Arguing against this explanation, we found that wrrs and chutters occurred together in only 27% of all intergroup encounters observed ($N = 113$), and that wrrs and chutters from the same individual, which produced the strongest evidence for transfer of habituation (see above), occurred together in only 3% of all encounters (Cheney & Seyfarth, 1988). Results suggest, instead, that when one vervet monkey hears another vocalize, the listener forms a representation of what that call means. And if, shortly thereafter, the listener hears a second vocalization, the two calls are compared not just according to their acoustic properties, but according to their meanings.

This is not to say that monkeys are aware of the distinction between signs and the objects they denote, nor that they are aware of their ability to compare vocalizations according to their referents. We cannot assume that an individual who can make same/different judgments about two vocalizations on a habituation test will be able to make active use of this distinction. Indeed, Oden, Thompson, and Premack (1990) found that chimpanzees who could perceive a relational distinction when tested with a habituation procedure were nevertheless unable to apply their apparent knowledge of this distinction in a match-to-sample test. Habituation data alone, therefore, do not prove that the monkeys understand the relation "*wrr* denotes another group."

Although monkeys do seem to form some sort of mental representation of the objects and events denoted by their calls, it is important to emphasize how little we know about these representations. At this stage, for example, it is unclear precisely how the monkeys' representations might differ from associations formed through classical conditioning (e.g., Dickinson, 1980; Rescorla, 1988). Similarly, we cannot specify how much information is contained within a representation, how the information is structured, or how it is coded in the nervous system. We discuss an associative, representational account of these results more fully in the General Discussion.

Most speculatively, we must consider the possibility that some representation of another animal's mental state is involved in call production or perception. Do callers vocalize not just to affect listeners' behavior but to influence what listeners know about the environment? Do listeners treat vocalizations not just as signals about external referents but also as representations of the caller's knowledge? Some recent studies have begun to examine these issues.

THE ATTRIBUTION OF MENTAL STATES BY CAPTIVE MACAQUES

In a preliminary investigation of mental state attribution in monkeys, we carried out experiments on four captive groups of rhesus and Japanese (*Macaca fuscata*) macaques. In their natural habitats, rhesus and Japanese macaques live in groups that are larger but similar in composition to groups of vervet monkeys. By studying monkeys in large outdoor enclosures, we were able to maintain relatively natural social groups while simultaneously providing some individuals with information that others did not possess.

The subjects were adult females and their 2- to 3-year-old offspring. In the *knowledgeable* condition, mother and offspring were seated next to one another in a chute that led into a large circular arena. In one experiment, both were able to observe a technician place apple slices into a food bin in the empty arena. In a second experiment, both observed a technician approach with a capture net and hide behind a wall close to the arena. In the *ignorant* condition, an opaque partition separated the mother from her offspring, and only the mother could see the food bin being filled or the threatening technician hiding. In both the knowledgeable and the ignorant conditions, after the food had been placed in the bin or the technician-predator had concealed himself, the offspring, but not the mother, was released into the arena.

If monkeys are sensitive to the mental states of others, mothers should have uttered more calls (or in some other way altered their behavior) when their offspring were ignorant than when they were already informed. If, however, monkeys are unaffected by their audience's mental states, the mothers' behavior should have been similar regardless of whether or not their offspring had already seen the food or danger.

As expected, the juveniles' behavior was strongly affected by whether they were ignorant or knowledgeable of the food or threatening technician. In the knowledgeable condition, they either quickly obtained the apple slices or huddled close to the escape chute, away from the wall that hid the technician. In the ignorant condition, they often failed to obtain the food, and they showed no heightened fear response. In contrast, there were no differences at all in the mothers' behavior under the two conditions (Cheney & Seyfarth, 1990a). Mothers failed to give more alarm calls or in any other way change their behavior when their offspring were ignorant as opposed to knowledgeable.

Discussion

Results suggest that mothers failed to take into account their offsprings' mental states when communicating with one another. The experiments are not, however, satisfactory or definitive, for two reasons. First, even if mothers had selectively alerted their offspring about food or danger, we would not be able to conclude that they did so because they recognized in their offspring a mental state different from their own. They could just as easily have been responding to the offsprings' behavior. Second, the negative results that we did obtain do not allow us to distinguish between an inability to attribute states of mind to others and a failure to make use of such an ability. It remains possible that monkeys do recognize the difference between their own knowledge and the knowledge of others, but that this recognition simply has no effect on their behavior. However, if rhesus and Japanese macaques are capable of distinguishing ignorance and false beliefs in others, their apparent failure to act on this knowledge is striking.

Research by Povinelli, Parks, and Novak (1991, 1992) supports the view that monkeys cannot represent the knowledge of other individuals. A similar conclusion emerges from Povinelli's more recent work with chimpanzees. Povinelli and Eddy (1996a, 1996b, 1996c) suggest that, while chimpanzees can accurately track the gaze of others and use gaze direction to obtain information about their surroundings, they are not simultaneously aware of the mental states in others that underlie their attention.

Povinelli's studies of captive apes have typically involved training—often extensive—followed by tests of a chimpanzee's ability to attribute one or more mental states to a human. Taking a different, complementary approach to the same problem, we review below some recent studies that consider mental state attribution in free-ranging baboons. Although limited because they deal with monkeys rather than apes, these tests have two advantages. First, they avoid the complications introduced by training. Second, if any animal *can* attribute mental states to another, and if—as seems likely—this skill is restricted to conspecifics and to interactions that occur within certain domains (e.g., Humphrey, 1976), then field experiments involving conspecifics provide the context in which mental state attribution is most likely to be revealed to the experimenter.

BABOON CONTACT BARKS

When they are dispersed and moving through wooded areas, baboons (*Papio cynocephalus ursinus*) living in the Okavango Delta of Botswana often give loud barks that can be heard up to 200 m away. The barks form an acoustically distinct class of vocalizations that cannot be confused, either spectographically or by ear, with other calls in the baboons' repertoire. Because contact barks are often temporally clumped, with many individuals giving calls at roughly the same time (Cheney, Seyfarth, & Palombit, 1996), the baboons appear to be answering one another. Like the loud calls of many other nonhuman primates (e.g., Boinski, 1991; Byrne, 1981; Kudo, 1987), baboon barks seem to serve as "contact" calls that maintain group cohesion, initiate and set the direction of the group's movement, and prevent individuals from becoming lost. In some species, loud long-distance calls may also serve as conditional recruitment signals that attract others to food. For instance, foraging subgroups of spider monkeys, *Ateles geoffroyi* (Chapman & Levebre, 1990), and chimpanzees, *Pan troglodytes* (Clark & Wrangham, 1994; Wrangham, 1977), frequently give loud calls upon arriving at food resources. Typically, more calls are given at large food patches than at small ones.

Despite these observations, there is some doubt about whether loud calls have evolved specifically to alert others to food or to maintain contact between separated group members. For example, although calling subgroups of spider monkeys are joined by other monkeys three times as often as subgroups that remain silent, even calling subgroups are joined only 17% of the time (Chapman & Levebre, 1990). Among chimpanzees, parties that call are not joined more than parties that remain silent (Clark & Wrangham, 1994). Chimpanzees do not call more at times of high fruit production than at other times, and chimpanzees that fail to alert others to food are not obviously punished. Because high-ranking males give more loud calls than do other individuals, Clark and Wrangham have suggested that calling functioned to signal the caller's status rather than to alert others to food (see also Mitani & Nishida, 1993).

Analyses of chimpanzee pant hoots highlight a problem that is common to research on many animal vocalizations: although listeners can potentially use calls to maintain contact with signalers or to locate food, signalers may not call with the intent of informing others. To date, for example, no studies have shown that individuals 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 has recently been visited by many group members.

For those interested in establishing whether or not the attribution of mental states plays a causal role in communication, the mechanisms that underlie the production of "contact" barks are crucially important. An individual who attributes mental states to others recognizes that his own knowledge and beliefs may be different from theirs (e.g., Dennett, 1988). Hypotheses based on mental state attribution predict that a baboon, for example, will answer the contact calls of others even when he is in the center of the group progression and at no risk of becoming separated from others. By contrast, if a baboon is incapable of understanding that other individuals' knowledge can be different from his own, he should be unable to recognize when others have become separated from the group unless he himself is also at risk of becoming lost. The production of a contact call, therefore, will depend primarily upon his own circumstances (e.g., separated or alone) rather than on the circumstances of those whom he appears to be answering.

Observations

To test between these hypotheses, we gathered data on the social context of contact barks given by adult female baboons over a 3-month period (Cheney et al., 1996). The group's 23 females gave a total of 1,662 calls. Ninety-two percent (1,529) occurred in the 5 min following a call by another female, the caller herself, or both. The fact that a contact bark might be preceded by several contact barks, some given repeatedly by the same individual and some given singly by others, complicated efforts to determine the frequency with which females were expected to give "answering" contact barks. As a first, crude pass at investigating this question, we simply calculated expected frequencies on the basis of each female's representation in the group.

If females had given "answering" calls at random, 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 5 min following a contact bark by another female than would have been expected by chance (two-tailed binomial test, $p < .001$). Even close kin failed to answer each other's contact barks more often than would be 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 would be expected by chance ($p < .001$) (Cheney et al., 1996).

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.

Experiment

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 36 playback experiments (Cheney et al.,

1996) in which we played to subjects the contact bark of a close female relative (a mother, daughter, or sister).

In 19% of the trials, subjects did in fact "answer" their relative's contact bark by giving at least one bark themselves within the next 5 min. In one additional experiment, the subject called in the 7th min 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, revealed 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 2; $\chi^2 = 4.43, p < .05$). They were also significantly more likely to give answering barks when there was no other female within 25 m than if there was at least one other female nearby (Figure 1; $\chi^2 = 5.86, p < .05$).

Discussion

Although it is always difficult to determine the precise meaning of a call to signalers and recipients, some speculation about the function and meaning of baboon contact barks seems possible. First, long-distance calls that function to maintain contact among kin or any other subset of group members must necessarily be individually distinctive. In analyzing the acoustic features of contact barks (Cheney et al., 1996), we found many features that could have allowed a listener to distinguish between the contact barks of different individuals. Individuals could, therefore, potentially have exchanged calls selectively with particular other group members.

Second, when subjects responded vocally to playbacks of contact barks, they always responded by giving contact barks rather than some other type of call. In contrast, they never gave contact barks in response to playbacks of any other call types (see below). It therefore seems probable that females interpreted these barks as being restricted, in the information they conveyed, to the context of separation or loss of contact with others.

Third, both observations and experiments suggest 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 primate species, baboon contact barks appear to reflect the signaler's own state and position rather than the state and position of others.

An individual that calls to maintain contact with separated group members should answer the calls of others even when she is in the center or vanguard of the group progression. To answer others, however, an individual must be able to recognize that other animals can be at risk of losing contact with the group even when she herself is not. The fact that baboons do not selectively answer the calls of other individuals suggests that contact barks are not given with the intent of sharing information. Although the calls may function to allow individuals to locate and rejoin the group, their production depends primarily on the signaler's own attempts to maintain contact with particular other individuals. In this case, therefore, the in-

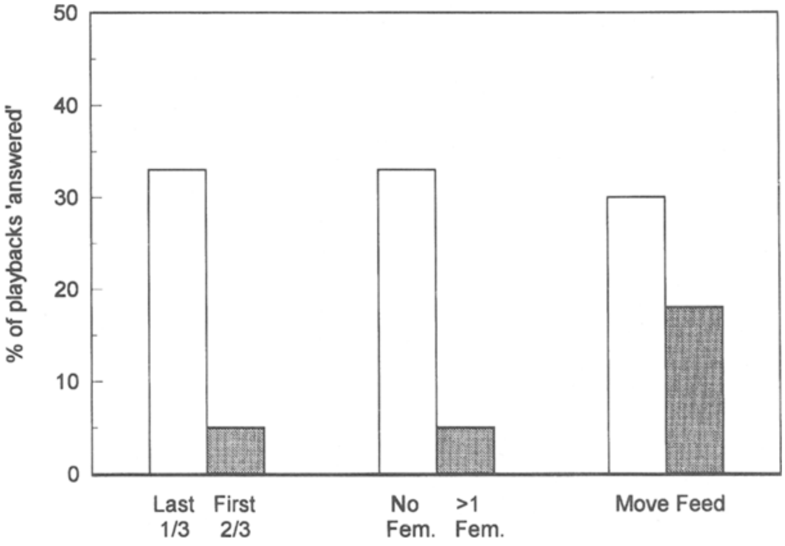

Figure 2. The proportion of playback experiments that elicited answering barks from subjects in different contexts. Histograms compare subjects in the last third versus the first two thirds of the group progression, in the vicinity of no other versus at least one other female, and moving as opposed to feeding. Data are based on 36 trials involving 18 subjects. From "The Functions and Mechanisms Underlying Baboon Contact Barks," by D. L. Cheney, R. M. Seyfarth, and R. A. Palombit, 1996, *Animal Behaviour*, *52*, p. 515. Copyright 1996 by Academic Press. Reprinted with permission.

formation extracted from the signal by listeners differs markedly from the information that the signaler "intended" to convey.

BABOON GRUNTS

Female baboons are rarely separated from their group, and as a result, contact barks occur at relatively low rates (<1 call/h among adult females). By contrast, the most common baboon vocalization—a low-pitched, tonal grunt—occurs more than 20 times as often. Although an adult female may grunt to another while foraging, resting, grooming, or in the minutes after aggression, grunting occurs at the highest rate during interactions involving young infants. Typically, one female approaches another who is carrying a young infant, grunts repeatedly, and touches, sniffs, or hugs the infant.

Grunts may be causally related to subsequent friendly interactions. In a study of the function of grunts in captive stump-tailed macaques (*Macaca arctoides*), Bauers (1993) found that individuals who grunted to mothers before attempting to handle their infants were less likely to receive aggression than those who remained silent (see also Bauers & de Waal, 1991). Grunts, it appeared, acted to signal benign intent and to facilitate social interactions. These observations suggest, but do not prove, that grunts and subsequent friendly interactions are causally related.

If grunts or other vocalizations do function to facilitate affinitive interactions, they might also be expected to play a role in reconciling opponents following aggression. Nonhuman primates, including baboons, 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 fights (e.g., Aureli, 1992; Aureli, van Schaik, & van Hooff, 1989; Cheney & Seyfarth, 1989; de Waal & Yoshihara, 1983; Judge, 1991; York & Rowell, 1988). 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. Only one study of captive long-tailed macaques (*Macaca fascicularis*), however, has demonstrated experimentally that apparently reconciliatory behavior does in fact function to restore opponents to baseline tolerance levels (Cords, 1992, 1993; Kappeler & van Schaik, 1992). Moreover, none of these studies considered the role that vocalizations might play in reconciling former opponents.

Below, we review data indicating that the grunts of adult female baboons act to mollify subordinate individuals and to facilitate social interactions (Cheney, Seyfarth, & Silk, 1995). Next, we describe a playback experiment designed to test the hypothesis that grunts lead to reconciliation, either by reducing the anxiety of victims (Cheney et al., 1995) or by altering victims' behavior toward their former opponents (Cheney & Seyfarth, in press).

Observations

We recorded 2,698 incidents in which 1 female approached another who ranked lower than herself; in 621 (23%) of these cases, the dominant female grunted to the subordinate. There were 17 females who could approach at least one lower ranking, unrelated individual. For 15 of the 17, the mean frequency of approaches to all possible partners who was followed by a friendly interaction was higher if the dominant female first grunted than if she did not (Figure 3a; one-tailed Wilcoxon matched-pairs signed-ranks test, 1 tie, $t = 1, p < .001$). 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 3b; $t = 10, p < .001$). Results were unaffected by the relative difference in rank between the 2 females. Grunts, therefore, appeared to mediate and facilitate social interactions among unrelated adult females.

To test whether grunts might also function to reconcile opponents after aggression, we sampled the behavior of aggressors and their victims. Whenever two females were involved in an aggressive interaction, we followed the aggressor for 10 min to determine whether she subsequently interacted with her victim in any way (Silk, Cheney, & Seyfarth, 1996). In 27 (5%) of 502 such samples, the aggressor subsequently interacted in a friendly manner with her opponent by touching her, grooming her, or interacting with her infant. Eighty-five percent of these friendly interactions also included a grunt by the aggressor. In 43 (9%) of the 502 samples, 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 affinitive interactions, might function to reconcile opponents. Nevertheless, the significance of the grunts themselves was difficult to assess simply from observations, because grunts so often occurred in conjunction with other friendly behavior, such as grooming or infant handling. To determine whether grunts might function to reconcile opponents even in the absence of other affinitive interactions, therefore, we designed a playback experiment (for details see Cheney et al., 1995).

Experiment 1

To begin, 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 min to determine whether she interacted affinitively with her opponent, and, if so, what form this affinitive interaction took. After this period, but within the next 30 min, 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 min in which A and B had not interacted.

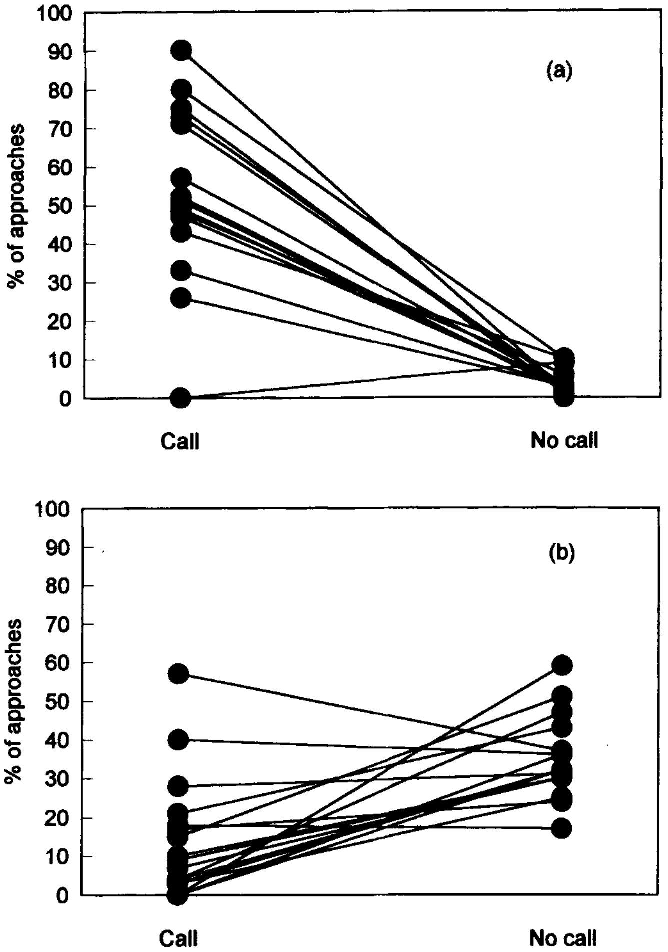

Figure 3. The mean proportion of 17 females' approaches toward subordinate partners that were followed by either (a) friendly behavior by the dominant or (b) a supplant of the subordinate. Approaches are divided according to whether the dominant female grunted as she approached or remained silent. Only interactions among unrelated females are included in the analysis. Additional analyses that considered each dyad separately yielded similar results. From "The Role of Grunts in Reconciling Opponents and Facilitating Interactions Among Adult Female Baboons," by D. L. Cheney, R. M. Seyfarth, and J. B. Silk, 1995, *Animal Behaviour*, *50*, p. 252. Copyright 1995 by Academic Press. Reprinted with permission.

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).

Our observations of baboons' responses to naturally occurring screams had indicated that females typically respond to the screams of unrelated, higher ranking females by either ignoring the call entirely or looking briefly (usually for <5 sec) in the direction of the call (Cheney & Seyfarth, unpublished data). We therefore used as our measure of response the duration with which subjects looked toward the speaker following the onset of the scream compared with the length of time during which they looked toward the speaker in the seconds before the scream was played. 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 4; one-tailed Wilcoxon matched-pairs signed-ranks test, $n = 15$, 1 tie, $t = 17.5, p < .025$). 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 4; $n = 15$, 1 tie, $t = 24, p < .05$). 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 4; $n = 15$, 2 ties, $t = 47.5$, n.s.).

There were 14 other dyads that met two of the three test conditions described above. For 7 dyads, "fight with no vocal reconciliation" could be compared with the "no prior interaction" control. For 7 other dyads, "fight with vocal reconciliation" could be compared with the "no prior interaction" control. Results from these trials further supported the 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 (fight with no interaction, 4.5 sec ± 2.4 sec; control, 1.2 ± 1.5 sec: $n = 7$, $t = 1, p < .01$). If, however, the dominant female had grunted to her opponent, the opponent's response was the same as after the control period (fight then grunt, 1.0 ± 1.2 sec; control 2.0 ± 1.6 sec: $n = 7$, 1 tie, $t = 3.5$, n.s.).

Some studies of macaques have suggested that proximity alone may serve a reconciliatory function (Cords, 1993; de Waal, 1989). 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 min 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 who had only been approached responded significantly more strongly than did subjects who had also received a grunt when they were approached (Mann–Whitney U test, $n_1 = 5, n_2 = 22$, $U = 22.5, p < .05$).

Discussion

Results suggest that baboon females' grunts function as reconciliatory signals because they reduce lower ranking females' anxiety after aggression. This conclusion, however, rests on two assumptions (Cheney & Seyfarth, in press): first, that a diminished response to an opponent's scream is an accurate reflection of reduced anxiety, and second, that reconciliation is appropriately defined in terms of reduced anxiety. Using similar reasoning, it has been argued that reconciliation functions to lower stress in captive groups of macaques because it decreases victims' scratching (Aureli & van Schaik, 1991) and heart rates (Smucny, Price, & Byrne, 1996).

To date, only one study of captive long-tailed macaques has shown that reconciliation has an effect on victims' subsequent behavior toward former opponents (Cords,

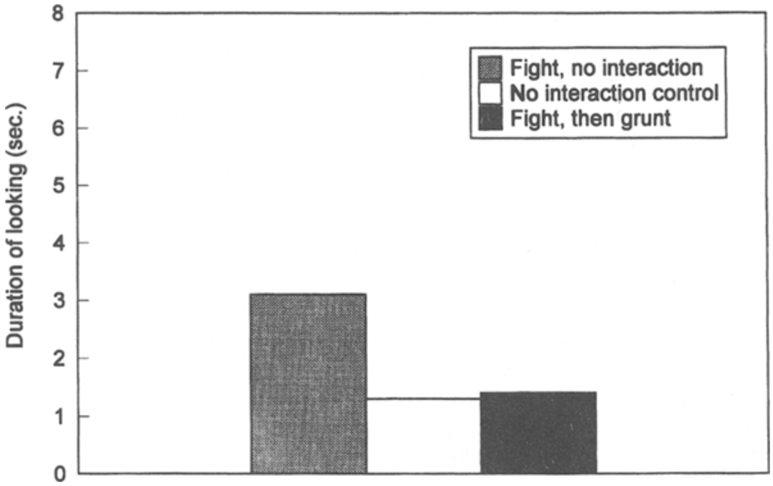

Figure 4. The duration of subjects' responses to the screams of dominant opponents after (1) the dominant threatened the subject and did not interact with her again; (2) the two females had not interacted for at least 90 min; and (3) the dominant threatened the subject and then reconciled by grunting to her. Histograms show means for 15 dyads in each of the three conditions. Subjects' responses were scored as looking in the direction of the speaker.

1992; see also Cords & Thurnheer, 1993). Even here, however, the interactions of former opponents may have been artificially influenced by the fact that the animals were forced into proximity with one another during the postconflict period.

A reconciliatory grunt could potentially affect a victim's behavior by increasing the probability that she would approach or initiate friendly behavior with her opponent. In principle, this hypothesis could be tested by following a subordinate female for some period of time after a fight and comparing her behavior after she received a reconciliatory grunt with her behavior after she did not. This procedure, however, is flawed, because grunts are so often given in association with other friendly behavior. The occurrence of other types of interaction makes it difficult to determine, through observation alone, whether a vocalization can function by itself to influence victims' behavior.

To circumvent this problem, we experimentally mimicked vocal reconciliation by playing the grunts of former opponents to victims in the minutes immediately following a fight. Our goal was to determine whether a "reconciliatory" grunt would not only reduce victims' anxiety but also influence their subsequent interactions with former opponents (Cheney & Seyfarth, in press).

Experiment 2

We conducted half-hour-long behavioral samples of females immediately after they had been threatened by a more dominant, unrelated female. During these samples, we noted the identities of all individuals who either approached or were approached by the victim, as well as all subsequent social interactions. Postconflict samples were conducted under three conditions. In the test condition, we played a tape-recording of the opponent's grunt to the victim as soon as possible following the fight (see below), in an attempt to mimic reconciliation (the "reconciliatory grunt" condition).

We compared the data obtained in the half hour following playback of a reconciliatory grunt with postconflict samples involving the same victim and the same opponent under two different control conditions. In the first control condition, the victim was played the grunt of a female who had not been involved in the fight (the "control grunt" condition) but had nonetheless been in the general vicinity (within 50 m) when the fight occurred. The female whose call was chosen for this control playback was always higher ranking than the victim, though she might be either higher or lower ranking than the opponent. Data collected following playback of a control grunt allowed us to determine whether a victim might change her behavior toward her opponent after hearing any higher ranking female's grunt, not just specifically her opponent's.

In the second control condition, we sampled the same victim for half an hour in the absence of any playback, to determine the victim's baseline probability of approaching her opponent (the "no vocalization" condition).

First interactions. Because these experiments were conducted on free-ranging animals, there were many postconflict samples when the victim and her opponent simply moved out of each other's vicinity and never interacted at all. In other cases, however, the victim and her opponent did subsequently come into proximity of one another. In 26 of the 35 dyads with postconflict samples in each of the three conditions, the victim and her opponent interacted at least once in the half hour following a "reconciliatory" grunt. For 15 dyads, the first interaction occurred either when the victim grunted to her opponent or approached her opponent to within 2 m. In no case did the same victims approach or grunt to their opponents in the half hour following playback of a control vocalization (two-tailed binomial test, corrected for ties, $n = 15$, $x = 0, p < .001$) or in the period following no playback at all ($n = 15, x = 0, p < .001$). For another 11 dyads, the first interaction occurred when the opponent approached to within 2 m of the victim but did not supplant her from the immediate vicinity (a "tolerated" approach). Again, the same victims did not permit tolerated approaches following playback of a control vocalization ($n = 12, x = 1$, $p < .01$) or following no vocalization at all ($n = 11, x = 0$, $p < .001$).

In contrast, when opponents approached their victims in the absence of a prior reconciliatory grunt, they typically supplanted them from the immediate vicinity (control vocalization versus reconciliatory grunt condition, $n = 4, x = 0$, n.s.; no vocalization versus reconciliatory grunt condition, $n = 10, x = 0, p < .01$). Results are summarized in Figure 5.

Although playbacks of reconciliatory grunts appeared to influence victims' propensity both to approach their opponents and to tolerate their opponents' approaches, this increase in proximity did not necessarily lead to subsequent friendly interactions. On 8% (3/38) of the occasions when a victim approached her former opponent following a reconciliatory grunt, either the victim or her opponent initiated a friendly interaction within the next minute. In contrast, a friendly interaction occurred on 48% of the occasions when an opponent made a tolerated approach of her former victim following a reconciliatory grunt.

Comparison of postconflict periods with baseline rates of interaction. As in the analysis of first interactions, "reconciliatory" grunts increased victims' propensities to attempt to interact with their former opponents. The mean rate that each victim approached or grunted to her former opponents in the half hour after hearing their reconciliatory grunts was higher than the mean rate at which she approached the same individuals under baseline conditions, in the absence of a fight (two-tailed Wilcoxon matched-pairs signed ranks test, $n = 20$, 3 ties, $T = 4, p < .001$). By contrast, such grunts had no effect on opponents' tendencies to approach their victims. This was probably due to the fact that most "reconciliatory" grunts were not actually produced by the opponents themselves, but instead mimicked through artificial playbacks.

When opponents did approach their victims during postconflict periods, however, victims were more likely to tolerate these approaches if they had recently heard an

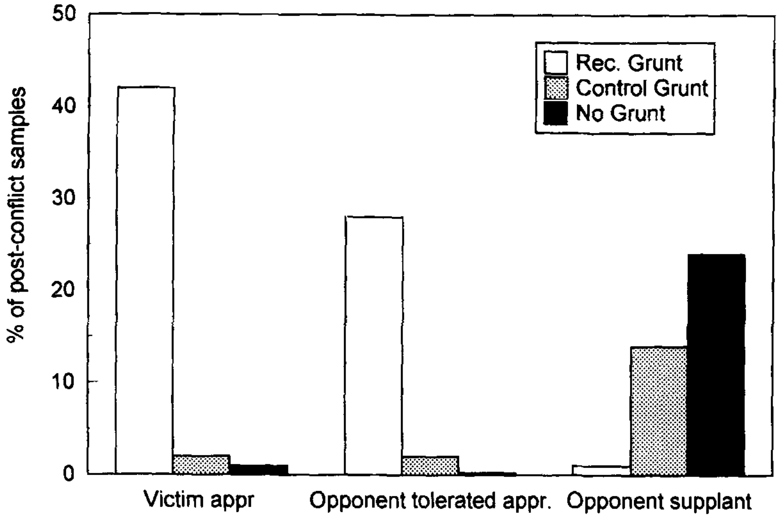

Figure 5. The proportion of first interactions between victims and their opponents that took various forms in each of three postconflict conditions. Histograms show means for all dyads taken together. Open histograms show victims' behavior following playback of a "reconciliatory" grunt; gray histograms show victims' behavior following playback of a control female's grunt; black histograms show victims' behavior in the absence of a playback trial. First interactions were defined as follows: Victim appr., the victim grunted to or approached her opponent to within 2 m; Opponent tolerated appr., the victim allowed her opponent to approach her without moving more than 2 m away; Opponent supplant, the opponent approached the victim and the victim moved more than 2 m away; Rec. Grunt, reconciliatory grunt condition. From "Reconciliatory Grunts by Dominant Female Baboons Influence Victims' Behaviour," by D. L. Cheney and R. M. Seyfarth, in press, *Animal Behaviour*. Copyright by Academic Press. Reprinted with permission.

apparently "reconciliatory" grunt than if they had not. Victims tolerated their opponents' approaches at higher rates following a reconciliatory grunt than under baseline conditions ($n = 20$, no ties, $T = 34, p < .005$). Similarly, victims were approached and supplanted by opponents at lower rates in the reconciliatory grunt condition than under baseline conditions ($n = 20$, 3 ties, $T = 1, p < .001$). Opponents threatened or chased their former victims on less than 4% of the occasions when they approached them.

In contrast, when victims were played either no vocalization at all or the vocalization of a dominant, uninvolved female, they approached their opponents at a significantly lower rate than they did under baseline conditions ($n = 20$, 2 ties, $T = 1, p < .001$). Similarly, they permitted tolerated approaches at a significantly lower rate ($n = 20$, 1 tie, $T = 1, p < .001$) and were supplanted by them at a higher rate ($n = 20$, 5 ties, $T = 18, p < .01$).

As in the analysis of first interactions, however, reconciliatory grunts did not increase the frequency of subsequent friendly interactions over baseline conditions (Cheney & Seyfarth, in press).

Discussion

These playback experiments highlight the different perspectives of signaler and recipient in any communicative event. Under natural conditions, reconciliation involves both motivation on the part of the dominant to interact with her former victim and recognition on the part of the victim of the dominant's behavior and/or motivation. Experiments that mimic vocal reconciliation allow us to analyze separately the behavior of signaler and recipient by observing what happens when from the victim's perspective reconciliation has occurred but from the dominant's perspective it has not.

Playback of "reconciliatory" grunts increased victims' propensities to approach their opponents but had no similar effect on opponents. Moreover, victims' approaches did not subsequently lead to an increase in the rate of friendly interactions relative to baseline rates, presumably because dominant females (who had not in fact reconciled with their opponents) were not motivated to participate in such interactions.

In contrast, when the dominant females themselves approached their victims following a reconciliatory grunt playback, victims were less likely to move away than they would have been had no vocalization occurred, and friendly interactions were more likely to follow. In these cases, apparently, reconciliation had occurred from the perspective of both animals.

What are the mechanisms that underlie production of a reconciliatory grunt? Are dominant animals motivated to change their victim's thoughts, beliefs, and desires, or do they simply want to interact with them or their infants? And on what grounds does a victim decide that her former opponent has reconciled? By judging her opponent's motivation, or by observing her behavior?

One explanation holds that dominant females give grunts in order to change the mental states of subordinates. As they approach, they grunt to alleviate the subordinate's anxiety even though they themselves, being dominant, are not anxious. After aggression, they grunt to reassure subordinates that they are no longer angry. This explanation accurately describes human appeasement or reconciliation; it has also been used by Goodall (1986), de Waal (1989), and others to explain the behavior of chimpanzees in a variety of different contexts. Two points argue against it, however.

First, though data on grunts are consistent with the hypothesis that dominant animals grunt to influence subordinates' mental states, we cannot rule out the simpler explanation that dominant animals grunt simply to affect subordinates' behavior. According to this explanation, a baboon that is approaching a more subordinate animal applies a contingency rule learned through past experience and perhaps also through observation: "Grunt, and animals won't move away." Similarly, when approached by a more dominant animal, they apply the following contingency rule: "When a dominant animal grunts, I can relax because I won't be attacked." Moreover, baboons could easily apply these rules selectively, grunting to subordinates with whom they want to interact (generally mothers with infants) and withholding grunts from those they want to supplant. In the laboratory, the production of primate vocalizations can readily be conditioned (reviewed in Pierce, 1985); in the wild, primates routinely approach, groom, play, and form alliances with some individuals but not others (reviewed in Smuts, Cheney, Seyfarth, Wrangham, & Struhsaker, 1987).

Second, although it seems likely that primates could learn to use vocalizations to affect other animals' behavior, there is very little evidence that individuals in any animal species ever take into account their audience's mental states when calling to one another. Baboon contact barks (see above) provide one example; for another, consider the production of antipredator alarm calls. In many species of birds and mammals, production of these vocalizations is not obligatory but depends on social context. Individuals readily give calls when in the presence of kin, for example, but withhold them 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, Karakashian, & Marler, 1986). Although this "audience effect" clearly requires that a signaler monitor the presence and behavior of group companions, it does not demand that the signaler also distinguish between ignorance and knowledge on the part of his audience. Indeed, in all species studied thus far, signalers 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.

In summary, the grunts used by baboons in appeasement and reconciliation modify not only the subordinate's affective state but also her behavior. It seems unlikely, however, that grunts are given with the intention of alleviating other individuals' anxiety and of repairing social relationships. Given the apparent inability of baboons to attribute mental states different from their own to others, it seems more probable that dominant females grunt to their victims because they wish to interact with them or their infants. Victims, in turn, learn through experience, and perhaps also by observing the interactions of others, that grunts honestly signal a low probability of aggression. Although a "reconciliatory" grunt may have the effect of changing the victim's mental state, it is probably not intended to do so.

GENERAL DISCUSSION

The Usefulness and Limitations of an Associative Account

Many of our results concerning the function of vocalizations in nonhuman primates are consistent with an associative account of behavior. For example, we assume that baboon grunts function to appease and to reconcile because listeners have learned, through experience, that if their opponent grunts she is unlikely to be aggressive, and baboon contact barks function to maintain group cohesion because listeners have learned, through experience, that barks provide information about the group's location. The questions of interest thus become, What processes underlie the formation of these associations? What is the nature of the animals' knowledge about features of the environment, and about the behavior and mental states of their companions?

Some current models of classical conditioning assume "that excitatory associations will be formed when the central representations of two or more events are activated concurrently" (Hall, 1996; see also Dickinson, 1980; Rescorla, 1987, 1988; Roitblat, 1987). According to this view, when presentation of an unconditioned stimulus (US) generates activity in a representation corresponding to that stimulus, and presentation of a conditioned stimulus (CS) generates activity in a second representation, the formation of an association between US and CS creates a link between the two representations such that presentation of the CS generates activity in the same representation activated by the US. Applying this terminology to our results, one might conclude that the sight of an eagle generates one representation in the mind of a vervet monkey; the sound of a vervet's eagle alarm generates a second representation; and that over time the association formed between the eagle and the alarm call causes the alarm call alone to activate the same mental representation (and elicit the same response) as does the sight of the eagle.

A second associationist view that does not require a mediating mental representation argues that vervet monkeys judge, for example, wrrs and chutters to be similar not because they activate the same mental representation but because they have, in the past, been associated with the same context and response (e.g., Wasserman & Astley, 1994). Testing between these two hypotheses is difficult, and we have no data that allow us to choose definitively between them. However, arguments that rely on a mental representation receive support from the following observation. When vervet monkeys hear an eagle alarm, it is not unusual to find some animals high in a tree, others on the open ground, and others in a bush. Animals in trees run down and out of them, animals on open ground look up into the air or run into bushes, and animals in bushes stay where they are (Seyfarth et al., 1980). One could argue that each individual has formed an association between alarm call and response that is highly specific and tightly linked to a particular microhabitat. A simpler explanation assumes that, upon hearing the alarm, each individual conjures up an image of the predator and then, on the basis of that representation, responds in an adaptive manner given its particular situation.

The Formation of Associations, and the Information That They Contain

If the association between a call and its putative referent were based on some simple, one-to-one mapping of a call's acoustic properties onto the physical properties of the referent, we would predict that calls with similar acoustic properties would designate similar referents and that subjects asked to make a same/different judgment between two vocalizations would base their comparison on the calls' acoustic features. Neither prediction is supported. Vervet monkeys, for instance, use four different grunts when approaching a dominant member of their group, when approaching a subordinate, when moving into an open area, and upon sighting another group. Their eagle alarm resembles these grunts in bandwidth and spectral features (Owren & Bernacki, 1988; Seyfarth & Cheney, 1984). The five call types are acoustically similar, but their referents differ markedly (see also Seyfarth & Cheney, 1997). In habituation/dishabituation experiments, a vervet monkey's response to an intergroup wrr or chutter depends on signaler identity, the information content of the call, and the listener's evaluation of that information, given recent events. Ordinarily, a female vervet becomes very vigilant upon hearing an intergroup chutter. However, if she has recently heard another, unreliable vocalization from the same caller that also denotes the presence of another group, she ignores the chutter.

These data suggest that although we cannot state precisely what mechanism leads to the association among neighboring groups, wrrs, and chutters, we can draw some conclusions about its characteristics. At the very least, the associative process cannot be based solely on the acoustic features of the two calls or on their prior temporal juxtaposition, and it must incorporate information about caller identity. One interpretation that is consistent with our data holds that the mental representations activated by the sounds of wrrs and chutters include some kind of image of the event—in this case, the approach or proximity of a neighboring group—as well as information about the individual who is vocalizing. Once such representations are formed, listeners judge the "meaning" of a vocalization not only by assessing the call's acoustic features but more importantly by comparing the representation activated by that call (its "meaning") with the representations activated by other, recently heard calls from the same individual.

We cannot, however, solve the philosophers' conundrum and state with any precision what sorts of concepts underlie vocalizations from either the signaler's or the recipient's perspective nor do our experiments allow us to conclude that two monkeys have the same thing in mind when one produces a call and the other responds to it. We can provide a partial answer to the problem by comparing responses of the same subjects to different vocalizations, or to vocalizations presented under different conditions. Vervet monkey leopard alarms apparently convey information that is different from the information conveyed by vervet eagle alarms, and the difference in information conveyed by these two calls is greater than the difference in information conveyed by vervet wrrs and vervet chutters. To female diana monkeys, the growl of a leopard and a male diana monkey's leopard alarm are more alike in meaning than either call is to the shriek of an eagle or a male diana monkey's eagle alarm. But these are indeed partial answers. Because we can only assess meaning by analyzing the responses that calls evoke, the precise meaning of nonhuman primate vocalizations remains elusive.

Information About Mental States?

Human speech provides us with information not only about referents external to the speaker but also about the speaker's thoughts and beliefs—his disposition to act in certain ways toward the referent. Part of our research has considered whether nonhuman primate vocalizations provide listeners with similar sorts of information—in other words, whether the representations activated by a vocalization, which clearly include information about the caller's identity and an external referent, also include information about the caller's mental state with regard to that referent.

In some cases, monkeys attending to each other's calls behave as if they were acquiring information not only about a signal's meaning but also about the signaler's mental state. If this conclusion could be supported, it would constitute a result of some significance, because communication in which the signaler and recipient are aware of each other's mental states is fundamentally different, more complex, and more powerful than communication in which the recognition of mental states is absent (Sperber & Wilson, 1986). However, whenever we are tempted to ascribe the attribution of mental states to monkeys, we cannot rule out alternative, simpler explanations.

For example, consider the reconciliatory grunts of baboons. If a dominant female grunts to a subordinate following an aggressive interaction, this grunt changes the subordinate's behavior. The subordinate is more likely to approach the dominant, and less likely to move away if the dominant approaches her, than she would have been had the dominant not grunted. The subordinate behaves as if she recognizes that the dominant's attitudes and intentions have changed since the initial fight occurred. An equally plausible (and certainly more parsimonious) explanation, however, posits that the subordinate simply responds on the basis of learned associations. Over time, she has learned that grunts are correlated with a reduced probability of attack. The information that listeners obtain when an individual vocalizes may be subtle and complex, but it need not include information about the signaler's knowledge or beliefs.

Studies of the contact, food, and alarm calls in other primate species point to similar conclusions (Kummer, Anzenberger, & Hemelrijk, 1996; see also Povinelli, 1993). Monkeys do not, apparently, make use of information about other animals' mental states even when it would be advantageous for them to do so. The lack of a "theory of mind" in nonhuman primates constitutes one of the fundamental differences between human language and animal communication (Cheney & Seyfarth 1990b, 1996).

Differences Between Signaler and Recipient

There is another way in which the representations formed in nonhuman primate communication differ from those that underlie human words. Adult human speakers are equally adept at learning to produce words and to understand them. By contrast, in nonhuman primate communication, the ease with which associative links are formed between calls and external events differs markedly, depending on whether the subject involved is producing or responding to a vocalization.

Consider, first, data from the listener's perspective. Results from at least two studies indicate that nonhuman primates can learn to associate almost any auditory stimulus with a particular social or ecological event. In the wild, vervet monkeys respond appropriately to the different alarm calls given by starlings (*Spreo superbus*) to ground and aerial predators (Cheney & Seyfarth, 1985); the development of this skill depends on experience (Hauser, 1988). In captive groups, immature rhesus and Japanese macaques who were cross-fostered and raised by another species have learned to recognize their mothers' vocalizations (and their mothers have learned to recognize theirs) even though the acoustic features of these particular calls differed from what the animals would normally have experienced (Seyfarth & Cheney, 1997).

In any communicative event, however, there are two associative links: the association formed by the caller between the initial stimulus and the caller's vocal response, and the association formed by the listener between that vocalization and the listener's subsequent behavior. And while the associations formed by listeners seem quite open-ended, the associations formed by callers are more innately constrained. Although callers can withhold or produce vocalizations voluntarily (Pierce, 1985), the acoustic features of vocalizations produced in any given context are highly predictable. The vocalizations used by vervets and baboons, for example, appear to be similar throughout the African continent, and it has proved notoriously difficult to document in nonhuman primates the kind of learned dialects found in birds (e.g., Payne, 1996). In the rhesus and Japanese macaque cross-fostering study mentioned above, cross-fostered juveniles continued to produce their own species' vocalizations despite being raised in an auditory environment that was different from the one that they would normally have experienced, and despite otherwise complete social integration into their adopted groups (Owren, Dieter, Seyfarth, & Cheney, 1983).

There is, then, a striking difference between the innate, developmentally constrained associations that apparently underlie call production and the labile, open-ended associations that underlie responses to vocalizations. This in turn suggests that the neural and behavioral mechanisms underlying primate communication—whatever they turn out to be—are likely to differ, depending on whether one is examining production or perception.

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