

# SIGNALERS AND RECEIVERS IN ANIMAL COMMUNICATION

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■ **Abstract** In animal communication natural selection favors callers who vocalize to affect the behavior of listeners and listeners who acquire information from vocalizations, using this information to represent their environment. The acquisition of information in the wild is similar to the learning that occurs in laboratory conditioning experiments. It also has some parallels with language. The dichotomous view that animal signals must be either referential or emotional is false, because they can easily be both: The mechanisms that cause a signaler to vocalize do not limit a listener's ability to extract information from the call. The inability of most animals to recognize the mental states of others distinguishes animal communication most clearly from human language. Whereas signalers may vocalize to change a listener's behavior, they do not call to inform others. Listeners acquire information from signalers who do not, in the human sense, intend to provide it.

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## INTRODUCTION

On a warm spring evening at the edge of a small pool of water in Panama, a male frog (*Physalaemus pustulosus*) gives his advertising call, onomatopoeitically described as a “whine” followed by a “chuck” (Ryan 1985). Almost immediately several things happen. In the mud nearby a smaller male of the same species, who has been calling with a whine alone, adds a chuck to his call (Rand & Ryan 1981). Simultaneously, a nearby female who had ignored the male giving a whine alone now becomes active. The female orients toward and then approaches the male giving the lower-pitched chuck (Ryan 1980, 1985). Ten feet overhead, a bat (*Trachops cirrhosus*) that has been circling the pond hears the frogs calling and dives down, flying directly at one of the calling males.

The evolution of calling in *Physalaemus* is now well understood. Male calls have been favored by natural selection to repel rivals and to attract females, while simultaneously minimizing the frogs’ susceptibility to predation by bats. The strongest frequency of a male *Physalaemus*’ whine-plus-chuck falls neatly within the range of the best hearing frequencies of males and females of the same species (Capranica 1977). The male’s call seems to have evolved to match the auditory system of its intended listeners (Ryan et al. 2001). Male *Physalaemus* are more likely to begin vocalizing if they hear a neighboring male give a whine-plus-chuck than if they hear a whine alone, and more likely to vocalize if the calling male is closer than if he is farther away. Males also give more acoustically complex calls as the number of calling males nearby increases (Ryan 1985). Females are attracted to the calls of males, and given the choice will approach whine-plus-chucks in preference to whines alone, and lower-pitched chucks in preference to higher-pitched chucks (Ryan 1985).

Calling by male *Physalaemus* is costly because it reveals the frog’s location to predatory bats. Presumably in response to predation pressure, natural selection has shaped the acoustic properties of whines so that they are difficult to locate (Ryan et al. 1982). Frogs add chucks to their whine because the chucks make them more attractive to females (Ryan 1980), but adding chucks also makes the frogs easier for bats to locate (Rand & Ryan 1981). Over evolutionary time, hard-to-find frogs and super-sensitive bats have engaged in an evolutionary arms race, and despite the frog’s best ventriloquial efforts some bats nonetheless manage to find their prey.

In functional terms, calling by male *Physalaemus* seems to have evolved with the goal of communicating as much as possible about the male’s size and condition to potential rivals and mates, while communicating as little as possible to bats. Note, however, that whereas this functional explanation provides a plausible scenario for the evolution of calling behavior in frogs, it reveals little about the proximate mechanisms that underlie a caller’s behavior and his listeners’ responses. Does the frog’s call produce its adaptive outcome because the caller “wants” to repel rivals or attract mates? When we describe the caller’s behavior as “goal directed,” do we really mean callers have a plan and monitor the outcome of their actions? Does the frog’s call achieve its result because nearby individuals assess and compare the

information conveyed by different calls, or are the responses of listeners reflexive, unthinking reactions to different stimuli?

The case of the bat is particularly instructive because the evolutionary tradeoffs are clear but the proximate mechanisms are not, and there is a striking difference between the interests of caller and recipient. From the frog's perspective, communication with bats is simply an unintended consequence of behavior that has evolved to deter rivals and attract mates. Although the frog has no goal of communicating to the bat, communication occurs nonetheless, as bats take advantage of a lucky accident and extract useful information from a signal that evolved for entirely different reasons. But does this mean that, when a bat hears a whine-plus-chuck it "thinks," or "conjures up images of," a frog even before it sees its prey? Or should we conclude more cautiously that the bat responds simply because it has, in the past, been reinforced for seeking food whenever it hears a particular sound?

In this chapter we discuss some recent research on the mechanisms that underlie vocal communication in animals. Our review is not meant to be exhaustive, either conceptually or taxonomically (for recent reviews see Hauser 1996, Bradbury & Vehrencamp 1998). Instead, we focus on several issues that allow us to make direct comparisons between animal communication and human language and between animal and human cognition.

## EVOLUTION

The example above illustrates two important themes of this review. First, communication is first and foremost a social event, designed to influence the behavior of listeners. Second, despite the social nature of communicative signals, the meaning and function of signals from the listener's perspective may be fundamentally different from that of the signaler's (Marler 1961).

The social function of communication is made clear by the fact that signalers rarely call except when in the presence of a potential audience. For example, in a modern modification on Tinbergen's classic (1951) experiment, Marler and colleagues presented male jungle fowl (*Gallus gallus*) with a silhouette of a hawk that "flew" over the birds' cage on a wire. The roosters gave alarm calls at high rates whenever they were in the presence of a male or female of their own species but almost no alarm calls when they were alone (Gyger et al. 1986, Karakashian et al. 1988). Even if calls emerge as involuntary expressions of the signaler's emotions, therefore, their production depends strongly on the proximity of listeners. At the same time, selection has also acted on listeners' ability to extract as much information as possible from both the signal itself and the context in which it is given. In some cases, like that of the bat described above, the information extracted by listeners comes at a significant cost to the signaler.

In aggressive interactions, in which signaler and recipient have largely competing interests, natural selection appears to have favored signals with acoustic properties that make the signals aversive to opponents (Owren & Rendall 2001),

or that accurately signal large size (Ryan 1985, Ryan & Brenowitz 1985) and a willingness to fight (Enquist 1985; reviewed in Bradbury & Vehrencamp 1998, p. 702). By signaling truthfully, large, dominant signalers can defeat opponents—and smaller, subordinate signalers can retreat—with minimal risk of injury. In some cases selection may have favored “deceptive” signals, uncorrelated with actual size or fighting ability, that succeed in driving away opponents as long as they are used only rarely (reviewed in Johnstone 1997). In all of these circumstances, selection appears to have favored signalers who can exploit the sensory abilities of their opponents, who accurately signal competitive skill when it is to their advantage to do so, and who bluff when doing so allows them to win with minimal cost. Simultaneously, selection appears to have favored recipients who are skilled in distinguishing those signals that genuinely reflect their opponents’ competitive ability from those that do not.

In more cooperative contexts, in which the evolutionary interests of signaler and recipient overlap to a greater degree, selection appears to have favored recipients who are skilled in extracting information and signalers whose behavior makes it easy for them to do so. The production and perception of alarm calls offers a good example. Producing alarm calls is potentially costly because calls may reveal the location of both the signaler and the signaler’s group to predators (e.g., Sherman 1977, 1980; Zuberbuhler et al. 1997). Despite this cost, alarm calls appear to have evolved both because they alert kin to the presence of danger (e.g., Sherman 1977, 1985) and because in some cases they also signal to predators that they have been detected (e.g., Zuberbuhler et al. 1999b). The number of acoustically distinct alarm calls in a given species’ vocal repertoire also appears to be under strong selective pressure. As we discuss below, species that are hunted by predators whose hunting techniques demand qualitatively different escape strategies give more acoustically different alarm calls than species that use similar escape strategies for all predators. Simultaneously, selection has favored listeners who can rapidly decode these signals and respond appropriately to them.

In both competitive and cooperative interactions, different cognitive mechanisms may underlie signal production and perception [for a similar perspective applied to the communication of human emotions, see Russell et al. 2003 (this volume)]. In many species call production appears to be a reflexive, affective reaction to a particular stimulus. By contrast, the mechanisms underlying call perception may be very different. The close link between eliciting stimulus and call type in signalers allows listeners to extract subtle information from vocalizations, and perhaps also to form a mental representation of a call’s meaning that affects the listener’s subsequent behavior. In many species the information that listeners extract from vocalizations can be studied using experiments that offer insights into the selective value and evolution of some of the cognitive mechanisms underlying communication.

While the asymmetry between signaler and recipient is one major theme of this review, a second concerns the cognitive limitations that affect both signaler and recipient and that constitute a fundamental difference between animal

communication and human language. The limitations arise, we argue, because most animals—with the possible exception of chimpanzees (*Pan troglodytes*; see below)—cannot attribute mental states to others (Cheney & Seyfarth 1990a, 1998; Seyfarth & Cheney 1997). As a result, whereas signalers call in response to many stimuli, including the overt expression of emotion in others, they seem not to produce calls in response to the perception of another animal's mental state such as knowledge or ignorance, which may not have any overt manifestation. And whereas listeners extract subtle information from vocalizations, they seem not to recognize that signals are reflections of the signaler's knowledge.

## COMMUNICATION FROM THE SIGNALER'S PERSPECTIVE

### The Stimuli that Elicit Vocalizations

What causes an individual to produce a vocalization? A number of different possibilities come to mind. Calls might be elicited by the sight of a particular stimulus, such as a predator, or by a particular sound, such as the call of a conspecific. In many species calls of a particular type are given only in distinct social or ecological circumstances, for example when interacting with a particular individual or foraging in dense vegetation. To gain a complete understanding of the mechanisms that underlie call production, we need to conduct experiments in which eliciting stimuli are manipulated and the production of a particular vocalization is the dependent variable. Such tests have been rare, however, largely because it is difficult to duplicate the complex social and ecological conditions that elicit vocalizations under natural conditions.

Some animal vocalizations are elicited by a broad array of stimuli, whereas others are highly stimulus specific. For example, both suricates (*Suricata suricatta*, a South African mongoose), and female diana monkeys (*Cercopithecus diana*) give "alert" calls to a large variety of stimuli, including mammalian and avian predators, large nonpredatory animals, falling trees, and social disturbances within the group (Gautier & Gautier 1977, Zuberbuhler et al. 1997, Manser 1998). These general alerting signals stand in marked contrast to the more acoustically distinct calls that individuals of the same species give to specific types of predator. Suricates, for example, give one alarm call type to mammalian predators, primarily jackals (*Canis mesomelas*), a second alarm call type to avian predators, primarily the martial eagle (*Polemaetus bellicosus*), and a third alarm call type to snakes such as the Cape cobra (*Naja nivea*) and to fecal, urine, or hair samples of predators and foreign suricates (Manser 2001). Diana monkeys give acoustically distinct alarm calls to mammalian predators such as leopards (*Panthera pardus*) and to avian predators such as the crowned eagle (*Stephanoetus coronatus*) (Zuberbuhler et al. 1997, 1999a).

In some species with predator-specific alarm calls, variation in predator type is the primary stimulus that determines which alarm call is given. Variation in other

aspects of the social and ecological context are relatively unimportant. In vervet monkeys (*Cercopithecus aethiops*) and diana monkeys, for example, the sight or sound of a leopard or eagle elicits the appropriate alarm call, and the close link between eliciting stimulus and alarm call type is largely unaffected by variation in predator numbers, distance, elevation, or the immediacy of attack (Seyfarth et al. 1980, Zuberbuhler 2000).

In other cases the relation between eliciting stimulus and alarm call type is more complex. In suricates, for example, signalers also vary the acoustic properties of each alarm call type to signal levels of urgency (Manser 2001). Thus, for example, a low-urgency mammalian predator alarm call is not only acoustically different from a low-urgency avian predator alarm call but also from a high-urgency mammalian predator alarm call. Listeners respond in qualitatively different ways to different alarm call types and, within each alarm call category, in different ways to calls correlated with different levels of urgency (Manser et al. 2001). The eliciting stimuli for suricate alarms, therefore, include both predator type and some features of the immediate context that seem to be correlated with the caller's perception of urgency (Manser et al. 2002). Evans et al. (1993) discuss the necessary and sufficient cues for the elicitation of alarm calls in chickens. Fischer et al. (1995) provide other examples of calls that simultaneously encode information about specific external stimuli and urgency.

In California ground squirrels (*Spermophilus beecheyi*) and marmots (*Marmota flaviventris*), ecological context overrides predator type as an eliciting stimulus. If a predator arrives suddenly and there is little time to escape, California ground squirrels give "whistle" alarms regardless of whether the predator is a terrestrial mammal or a raptor. When a predator is spotted at a distance, squirrels give "chatter-chat" alarms, again regardless of predator type (Leger et al. 1980, Owings & Hennessy 1984; see also Blumstein & Armitage 1997 for similar data on marmots).

Studies of the "audience effect" in animal vocalizations demonstrate further how call production can depend on a combination of certain narrowly defined stimulus features (such as the predator) and other, equally specific contextual cues. As noted earlier, roosters give more alarm calls when paired with a member of their own species than when either alone or paired with a member of another species (Marler et al. 1990). Similarly, in ground squirrels alarm call production is strongly influenced by the presence or absence of kin (Sherman 1977; see also Cheney & Seyfarth 1990a for similar data on vervet monkeys).

Like predator alarm calls, most vocalizations given by animals during social interactions are elicited by a complex combination of stimuli. For example, the most common vocalization given by free-ranging baboons (*Papio cynocephalus ursinus*) is a low amplitude tonal grunt, which is produced in a variety of social contexts. One, the move grunt, is typically given when the group is about to initiate a move into a new area of its range. Move grunts are given in bouts of 1–2 calls and often elicit answering move grunts from others nearby. By contrast, infant grunts are given during friendly social interactions, for example, as the caller approaches a mother with an infant and attempts to touch or handle the baby. Infant grunts

are given in bouts of 5–10 calls and seldom elicit answering grunts (Cheney et al. 1995a, Owren et al. 1997). Both call types are individually distinctive (Owren et al. 1997). Moreover, although grunts are acoustically graded, typical move grunts show subtle acoustic differences from typical infant grunts. Playback experiments conducted by Rendall et al. (1999) examined the stimuli that elicited vocal answers to move grunts and found an effect of both call type (vocal responses were more likely when the playback stimulus was a move grunt than when it was an infant grunt) and social context (grunt responses were more likely in the move than in the rest context). There was also an interaction between grunt type and context, with the majority of answers elicited by move grunts presented in a move context.

In many cases the elicitation of a vocalization or other communicative signal depends on both the immediate features of the social environment and the history of interactions between the individuals involved. Adult female squirrel monkeys (*Saimiri sciureus*) give “chuck” calls to one another when grooming, but only if the two females involved have a long-term, stable grooming relationship (Smith et al. 1982). Dominant female baboons occasionally grunt to a subordinate after an aggressive interaction, and such grunts seem to function as reconciliatory signals that restore the individuals’ relationship to baseline levels of tolerance (Cheney et al. 1995a, Silk et al. 1996, Cheney & Seyfarth 1997). In the competitive displays of many species, opponents’ signals are influenced both by their own motivation to attack and the responses elicited by their previous signals (e.g., Waas 1991).

**THE SPECIFICITY OF CALL PRODUCTION** When a vocalization with specific acoustic features is elicited only by a narrow range of stimuli and is relatively uninfluenced by other contextual factors, the call has the potential to provide listeners with very specific information. For example, the eagle alarm calls of vervet monkeys are elicited almost exclusively by raptors (Seyfarth et al. 1980). They are rarely given to stimuli other than raptors, and these species rarely elicit any vocalizations other than eagle alarm calls. Under these circumstances, eagle alarm calls have the potential to provide reliable information about the presence of a specific predator type. Through processes that may be similar to those that produce associative conditioning in the laboratory, listeners who have learned the predictable relation between eliciting stimulus and alarm call type can recognize immediately upon hearing an eagle alarm call that a raptor has been spotted, even if they have no other supporting, contextual cues. (Cheney & Seyfarth 1990a, Seyfarth & Cheney 1997; see also Owren & Rendall 1997).

Two factors determine the extent to which a vocalization can provide listeners with specific information. First is the call’s informative value. If call type A is elicited by eagles and eagles rarely appear without eliciting call type A, then the call has the potential to provide listeners with reliable information about the presence of an eagle. In the terms of associative, or Pavlovian, conditioning, the call is a conditioned stimulus (CS) and the eagle is an unconditioned stimulus (US). The informative value of the CS lies in the extent to which it accurately predicts the US. To be predictive, simple contiguity between call and predator is neither necessary

nor sufficient (Rescorla 1988). Instead, prediction and information depend upon the difference between the probability of a US when the CS is present and the probability of the US when the CS is absent (Gleitman 1991, p. 127). In suricates, the probability of an eagle being present when listeners hear an eagle alarm is very high; the corresponding probability when listeners hear no eagle alarm is very low. Eagle alarms are thus highly informative about the presence of an eagle.

The second important variable is the breadth of stimuli that elicit a given call type, defined as the call's referential specificity. Suricate eagle alarms are predictive (and thus informative) not only about the presence of an eagle but about the presence of specific species of eagle, because suricates give eagle alarms to only three species: martial eagles, tawny eagles (*Aquila rapax*), and (rarely) pale chanting goshawks (*Melierax canorus*) (Manser 2001). The suricates' eagle alarm is therefore a CS that is potentially informative about a very narrow range of USs. By contrast, the suricates' mammalian predator alarm is equally informative in Pavlovian terms but not as referentially specific, because mammalian predator alarms are given to a wider variety of stimuli, including jackals, hyenas, African wild cats, lions, and dogs (Manser 1998). A suricate eagle alarm potentially informs listeners that one of three species has been detected; a suricate mammalian predator alarm potentially informs listeners that one of at least five predators is present. Still less precise is the suricates' alert call (see above), which provides listeners with information that is rather vague. The alert call is a CS for which the associated US is a wide variety of predators, other suricate groups, large nonpredatory animals, and within-group social disturbances. The CS-US link between alert call and eliciting stimuli may well be as strong as it is between eagle alarm and eagle, but the variety of stimuli for which this rule holds is extremely broad.

Like alarm calls, the vocalizations given during foraging or social interactions vary in their informative value and referential specificity. Baboon move grunts, for example, are individually distinctive and produced only when the group is moving, about to move, or has just begun a move from one location to another (R. Seyfarth & D. Cheney, personal observation; Rendall et al. 1999). Move grunts are particularly likely to be given in three circumstances: in the last few minutes of a rest period when the group is about to move and some individuals have already begun to do so; in the first few minutes after all individuals have begun to move; and as an answering call in the seconds immediately after another individual has produced a move grunt. A group's transition from resting to moving seldom occurs without at least one move grunt (R. Seyfarth & D. Cheney, personal observation). Move grunts are, therefore, highly informative because they accurately predict the onset of a group move and referentially specific because the breadth of stimuli that elicit them is relatively narrow.

By comparison, the infant grunts of baboons have a lower informative value than move grunts for two reasons. First, when infant grunts are heard (CS), the probability of infant handling (US) may be high, but infant handling also occurs in the absence of grunts (Cheney et al. 1995a). Second, infant grunts are elicited in



many contexts that may not involve infant handling; for example, during friendly interactions between females without infants or as reconciliatory signals after aggression (Cheney et al. 1995a, Silk et al. 1996). Compared with move grunts, then, infant grunts are less informative because they are less predictive of infant handling and less referentially specific because the range of stimuli that elicit them is relatively broad. Infant grunts potentially provide listeners with information that a friendly social interaction is occurring, but they do not specify the precise type of social interaction.

In sum, the strength of association between call and eliciting stimulus (informative value) plus the breadth of eliciting stimuli involved (referential specificity) interact to determine the specificity of call production: the extent to which a call has the potential to convey precise information to listeners. Because they are strongly associated with a very narrow range of eliciting stimuli, some calls are highly specific and thus have the potential to transmit very precise information. Other calls are less contextually specific, and therefore have the potential to transmit less precise information, either because the association between call and eliciting stimulus is strong but the array of stimuli for which the association holds is relatively broad, or because the association between call and eliciting stimulus is weak. Finally, the specificity of call production says nothing about whether the vocalization actually does convey specific information to listeners; it simply describes the call's potential for doing so.

## Referential Versus Affective Communication: Apples and Oranges

Vocal communication in animals is generally thought to differ from human language largely because the former is an "affective" system based on emotion, whereas the latter is a "referential" system based on the relation between words and the objects or events they represent. Over the years, much ink has been spilled—by ourselves and others—debating whether animal vocalizations could ever have a referential component and, if so, how referential and affective signaling might interact (Seyfarth et al. 1980, Cheney & Seyfarth 1990a, Marler et al. 1992, Hauser 1996, Macedonia & Evans 1993, Evans 1997, Owren & Rendall 1997, Owings & Morton 1998, Fischer & Hammerschmidt 2001). Often the debate has been cast as an either/or opposition between affective and referential signaling. Such a dichotomy, however, is logically false.

A call's potential to serve as a referential signal depends on the specificity of call production, as discussed above. The mechanisms that underlie this specificity are irrelevant. A tone that informs a rat about the imminence of a shock, an alarm call that informs a vervet about the presence of a leopard, or a scream that informs a baboon that her offspring is involved in a fight all have the potential to provide a listener with precise information because of their predictable association with a narrow range of events. The widely different mechanisms that lead to this association have no effect on the signal's potential to inform.

Put slightly differently, there is no obligatory relation between referential and affective signaling. Knowing that a call is referential (that is, has the potential to convey highly specific information) tells us nothing about whether its underlying cause is affective or not. Conversely, knowing that a call's production is due entirely to the caller's affect tells us nothing about the call's potential to serve as a referential signal. As Premack (1972) argued, a shout that is entirely based upon affect—e.g., a cry of delight at the sight of strawberries—can serve just as referential a function as the word “strawberries” as long as the shout is predictably elicited by strawberries and no other stimuli.

It is therefore wrong, on theoretical grounds, to treat animal signals as either referential or affective, because the two properties of a communicative event are logically distinct and independent dimensions. The first concerns a signal's relation to features of the environment, whereas the second concerns the underlying mechanisms by which that relation arises. Highly referential signals could, in principle, be caused entirely by a signaler's emotions, or their production could be relatively independent of measures of arousal. Highly affective signals could be elicited by very specific stimuli and thus function as referential calls or they could be elicited by so many different stimuli that they provide listeners with only general information. In principle, any combination of results is possible.

The affective and referential properties of signals are also logically distinct, at least in animal communication, because the former depends on mechanisms of call production in the signaler, whereas the latter depends on the listener's ability to extract information from events in its environment. Signalers and recipients, though linked in a communicative event, are nonetheless separate and distinct, because the mechanisms that cause a signaler to vocalize do not in any way constrain a listener's ability to extract information from the call, a point highlighted by the bat's eavesdropping on the frog.

Baboon grunts offer a good example. In a recent study, Rendall (2003) used behavioral data to code a social interaction involving move or infant grunts as having high or low arousal. He then examined calls given in these two circumstances and found that in each context certain acoustic features or modes of delivery were correlated with apparent arousal. Bouts of grunting given when arousal was apparently high had more calls, a higher rate of calling, and calls with a higher fundamental frequency than bouts given when arousal was apparently low. Further analysis revealed significant variation between contexts in the same three acoustic features that varied within context. By all three measures (call number, call rate, and fundamental frequency), infant grunts were correlated with higher arousal than were move grunts. Infant grunts also exhibited greater pitch modulation and more vocal “jitter,” a measure of vocal instability (Rendall 2003). In human speech, variation in pitch, tempo, vocal modulation, and jitter are known to provide listeners with cues about the speaker's affect, or arousal (e.g., Scherer 1989, Bachorowski & Owren 1995).

It is, of course, difficult to obtain independent measures of a caller's arousal in the field. However, similarities between human and nonhuman primates in the

mechanisms of phonation (Schon Ybarra 1995, Fitch & Hauser 1995, Fitch et al. 2002) support Rendall's (2003) conclusion that different levels of arousal play an important role in causing baboons to give acoustically different grunts in the infant and move contexts. This view, however, says nothing about the grunts' potential to act as referential signals that inform nearby listeners about social or ecological events taking place at the time. As noted above, move grunts have the potential to convey quite specific information to listeners, and infant grunts less so.

Baboons also produce loud barks that vary acoustically from tonal, harmonically rich calls given at high rates when an individual is at risk of becoming separated from the group (contact barks), to noisy, harsh calls given when a predator has been seen (alarm barks; Fischer et al. 2001a). The gradation in acoustic features from clear (or tonal) to noisy suggests that barks reflect a gradation in the signaler's emotion (e.g., Morton 1977, Owren & Rendall 2001). Field playback experiments demonstrate that infant baboons respond differently, and with increasing intensity, to typical contact barks, intermediate barks, and typical alarm barks (Fischer et al. 2000), but adults show a distinctive response only to alarm barks. Apparently, adult responses to contact and intermediate barks are determined largely by context (Fischer et al. 2001b). These results suggest that, whereas different levels of arousal may indeed play an important role in causing baboons to give acoustically different barks in different contexts, certain barks nonetheless can provide listeners with specific information. Because they are given rarely and are limited to particular ecological contexts, alarm barks have a greater informative value and a higher referential specificity than contact barks. As a result, alarm barks elicit responses from listeners that are more consistent and less dependent upon context.

Taking a somewhat different approach, Manser (2001) coded interactions between suricates and their predators as either high- or low-urgency depending on the distance between predator and prey. As noted above, she found that the acoustic features of alarm calls varied depending on both predator type and apparent level of urgency. Moreover, the acoustic measures that accounted for variation across alarm call types were, for all but one measure, different from the acoustic measures that accounted for variation across levels of urgency. Calls given to different predators did not follow any apparent acoustic "rule": The acoustic features that distinguished mammalian predator, avian predator, and snake alarm calls followed no consistent pattern. By contrast, in all three call types low-urgency calls tended to be clearer and more harmonic, whereas high-urgency calls were harsher and noisier (Manser et al. 2001, 2002).

The production of suricate alarm calls may depend entirely upon the caller's state of arousal. High- and low-urgency calls are certainly correlated with acoustic features known to be associated with fear or anxiety in both animal vocalizations (Morton 1977, Hauser 1993, Owren & Rendall 1997) and human speech (Scherer 1989). In a similar manner, future research may ultimately show that the suricates' different alarm call types also reflect different levels of arousal, with one predator type eliciting the most fear, another the least, and the third intermediate. It may also turn out that suricates' alarms for different predators do not map easily onto

acoustic correlates of arousal. Whatever the outcome, the affective basis of call production is entirely separate from the calls' ability to convey specific information to others.

Acoustic variation of this sort, along two, largely uncorrelated dimensions, suggests that natural selection has acted simultaneously to favor calls that are correlated with urgency and calls that are correlated with predator type—just as selection has favored, in *Physalaemus* frogs, calls that simultaneously attract females and are as cryptic as possible to bats, and as selection has favored, in humans, speech that simultaneously provides listeners with referential information and information about the speaker's state of arousal. In all of these cases, questions about the emotions (or affect, or arousal) underlying call production are both empirically and theoretically separate from questions about a call's potential to convey referential information to listeners. We discuss this further below in "Communication from the Recipient's Perspective."

## Communication and Classification

When a specific call type is elicited by only a narrow range of stimuli, observers have the opportunity to study the mechanisms by which animals classify the elements that make up their environment. Many nonhuman primates appear to classify stimuli into groups that cannot be defined solely on the basis of shared physical features. Female diana monkeys, for example, respond to a male diana monkey's leopard alarm call and a leopard's growl with the same response: by giving their own, acoustically distinct, leopard alarm call. Similarly, females respond to a male diana's eagle alarm call and the sound of an eagle's shriek by giving their own eagle alarm call (Zuberbuhler et al. 1997). In habituation-dishabituation experiments, diana monkey females who first heard a male's leopard alarm call and responded to it with calls of their own were then tested, five minutes later, with the growl of a leopard coming from the same area. Under these conditions they no longer responded to the growl. They did respond, however, if they were tested with the shriek of an eagle (they gave eagle alarms). Similarly, females who first heard a male diana's eagle alarm call did not respond, five minutes later, to the shriek of an eagle but did respond with leopard alarms if they heard the growl of a leopard (Zuberbuhler et al. 1999a). Diana monkey leopard alarms and the growls of a leopard are very different acoustically, as are diana monkey eagle alarms and the shriek of an eagle. Nonetheless, the monkeys treat the two leopard-associated noises, and the two eagle-associated noises, as if they provide the same information.

One interpretation of these results argues that the mechanisms underlying call production include the formation of some internal representation about the eliciting stimulus, and this information determines whether or not a call will be produced. Upon hearing a male's leopard alarm, for example, a female diana monkey stores the information that a leopard is present, and this information causes her to give her own leopard-specific vocalization. Five minutes later, when she hears a leopard's

growl coming from the same location, she compares this new information with what she already knows. Because the new information is redundant, the female does not respond to the growl as she normally would, by giving an alarm call. Instead, she remains silent. Had the growl been an eagle's shriek, however, the female would have responded by giving her own eagle-specific vocalization.

The use of terms like "mental representation" and "information" in this account is similar to the use of a term like "memory" in other explanations of behavior. Upon hearing an auditory stimulus, a monkey is believed to store information that is specific to the stimulus. Later this information is retrieved and exerts a causal effect on behavior. Although we cannot at present specify the neural instantiation of this stored information, we use the terms mental representation and information as hypothetical, descriptive variables that may guide further research. For example, in this interpretation of the mechanisms underlying call production, there are parallels between the processing of calls by monkeys and the processing of words by humans. Just as humans respond to words by noting both their acoustic properties (auditory processing) and their meaning (semantic processing), monkeys process calls at two levels and can, in some circumstances, treat calls with different acoustic features as providing similar information (Cheney & Seyfarth 1990a, Zuberbuhler et al. 1999a).

The preceding interpretation finds parallels in modern animal learning theory (Dickinson 1980). If a rat learns that a light signals the imminence of shock, the rat begins to show fear and avoidance whenever the light comes on. In Rescorla's (1988) terms, the light provides the rat with "information" about the shock. Further, if a rat first learns that a tone is associated with the light and then learns that the light is associated with shock, it exhibits fear and avoidance behavior not only when the light comes on but also when the tone is heard, even though tone and shock have never been associated directly [Rizley & Rescorla 1972; see also Brogden (1939), who first described this phenomenon as "sensory preconditioning"]. Dickinson's (1980, p. 5) interpretation is that "during the first stage, exposure to the tone-light pairings set up some internal representation of this relationship [and] when the light subsequently acquired significance by being paired with the shock, the internal structure representing the tone as a predictor of the light resulted in the tone also becoming fear inducing." Though the light and the tone are qualitatively very different sorts of stimuli, and are processed by different sensory mechanisms, they have—like the leopard's growl and the diana monkey's leopard alarm call—come to elicit the same response because they provide the rat with similar information. Conditioning has led to "the learning of relations among events so as to allow the organism to represent its environment" (Rescorla 1988, p. 151).

Other explanations drawn from animal learning theory avoid terms like "information" and "internal representation." For example, Thompson (1995) suggests that, in experiments like those with diana monkeys described above, animals categorize conspecific leopard alarms and leopard growls as similar because the two calls have become associated with the same response and are therefore functionally

equivalent (see also Heyes 1994, Schusterman & Kastak 1998). In this formulation there is no need to assume that an animal has acquired information or that there is any internal representation of the relation between a call and some feature of the environment. Selective call production can be explained without any reference to mental events as causal agents.

At present there are no experiments that distinguish clearly between an explanation of call production based on information or internal representations and an explanation of call production based on association with a shared behavioral response. Below we consider the same issue as it applies to listeners (see "Communication from the Recipient's Perspective"), for which slightly more data are available. We also consider other arguments against the use of terms like "information" in animal communication (Owings & Morton 1998; Owren & Rendall 1997, 2001).

## Goals and Intentionality in Call Production

Animal vocalizations can be elicited by an extraordinary variety of auditory, visual, or olfactory stimuli (reviewed in Bradbury & Vehrencamp 1998). However, one class of stimuli apparently plays no role in eliciting calls from most nonhuman species. Its absence is interesting, because it is probably responsible for eliciting most of the vocalizations used in human conversation.

One function of language is to influence the behavior of others by changing what they know, think, believe, or desire (Grice 1957, Pinker 1994, Jackendoff 1994). When one person talks to another, he imputes mental states such as knowledge, beliefs, and goals to his listener. He assumes that the listener's mental states can be affected by what he hears and that these mental states will, in turn, affect the listener's behavior. Consequently, the speaker assumes providing the listener with information that alters what the listener knows may change the listener's behavior. A theory of mind is called a theory because, aside from introspection, humans have no direct evidence to support these assumptions (Premack & Woodruff 1978).

For humans engaged in conversation, the perception of another individual's mental state is perhaps the most common stimulus eliciting vocalization. By contrast, there is now growing evidence that, while animal vocalizations may have evolved because they can potentially alter the behavior of listeners to the signaler's benefit, such communication is—compared with human language—inadvertent, because signalers are unaware of the means by which vocalizations exert their effects. Male *Physalaemus* frogs call because calling causes females to approach and other males to move away. Even though females appear to choose among a number of males depending upon the pitch of their call (Ryan 1980, 1985), there is no evidence that a male frog calls because he attributes knowledge or desire to a female, or because he knows that his calls will affect a female's knowledge and that this knowledge will, in turn, affect her behavior.

Several observations and experiments, mostly with nonhuman primates, have attempted to determine whether the perception of another individual's mental state

ever serves as an eliciting stimulus for the production of vocalizations. In free-ranging vervet monkeys, infants often give eagle alarm calls to harmless species like pigeons. Typically, nearby adults look up, but rarely give alarm calls of their own. By contrast, when an infant is the first member of its group to give an alarm call to a genuine predator, adults often look up and give alarm calls themselves. In giving or withholding these second alarms, however, adults do not act as if they recognize the infant's ignorance and are attempting to inform the infant that he was correct: Adults give second alarms at similar rates regardless of whether the initial caller was an infant or another adult (Seyfarth & Cheney 1986).

These observations are supported by data on the production of loud calls among chimpanzees, who do not appear to adjust their calling to inform ignorant individuals about their own location or the location of food (Mitani & Nishida 1993, Clark & Wrangham 1994, Mitani 1996). Outside the domain of vocal communication, data on the development of tool use provide a similar picture. Although chimpanzees certainly differ from monkeys in the variety and frequency of tool use (McGrew 1994), there is no evidence that knowledgeable individuals ever actively instruct others (Caro & Hauser 1992) or treat ignorant individuals differently from knowledgeable ones (reviewed in Tomasello & Call 1997).

Both rhesus (*Macaca mulatta*) and Japanese (*M. fuscata*) macaques give alarm calls to predators (or maintenance staff when held in captivity) and coo calls upon finding food (Green 1975, Hauser & Marler 1993). Experiments with captive individuals, however, found no evidence that knowledgeable individuals were more likely to call when they were informed, but their offspring was clearly ignorant, about the nearby presence of a predator or food (Cheney & Seyfarth 1990b).

Free-ranging baboons often give loud "contact" barks when their group is widely dispersed in wooded areas. Because the barks are clumped in time, it often appears that animals are exchanging calls, and that some individuals are calling to inform others of their location. Playback experiments, however, offer no support for this interpretation. When adult female subjects were played an infant's contact bark from a distant loudspeaker, they were significantly more likely to orient toward the speaker if the infant was their own than if it was not. Clearly, females recognized callers individually. Infant identity, however, had no effect on the production of an answering vocalization by the female. Instead, call production depended primarily on the female's own state of separation from the group (Rendall et al. 2000; see also Cheney et al. 1996).

In sum, a variety of results argue that, in marked contrast to humans, nonhuman primates do not produce vocalizations in response to their perception of another individual's ignorance or need for information. This is not to say that calls cannot inform; to the contrary, we discuss below the many ways in which listeners obtain information from a caller who may not, in the human sense, have intended to provide it. Instead, the point to emphasize here is that many vocalizations whose production initially seems goal-directed are not, in fact, as purposeful as they first appear. Like the frog who inadvertently provides information to the bat, adult vervet monkeys inadvertently inform infants about the relation between alarm

call type and predator simply by producing alarm calls selectively themselves. Female baboons inform their infants and others within earshot of their own location simply by calling when they themselves risk being lost. At first glance, the frog's communication to the bat seems an inadvertent, evolutionary mistake: hardly a model for how animal communication works. Yet compared with human language, such inadvertent communication in animals may be much more common than previously realized.

## COMMUNICATION FROM THE RECIPIENT'S PERSPECTIVE

### What (if Anything) Is Communicated?

**BACKGROUND** Although the transfer of information from one individual to another is obvious in language, how can we know that it occurs in animals, where we cannot interview subjects and can only assess what an individual may have learned by observing its behavior? Early learning theorists noted that conditioning affects behavior but believed their methods did not allow them to draw conclusions about the intervening mechanisms, which might or might not involve the acquisition of information. Some even thought the notion of information, or knowledge, was irrelevant (Skinner 1974). Applied to the study of animal communication, this view finds parallels in Owren & Rendall's (1997) suggestion that "individual primates use vocalizations to produce affective responses in conspecific receivers" (1997, p. 307) and that "neither referential nor motivational information is necessarily encoded in such signals" (1997, p. 340). Owren (2000, p. 57) further concludes that "the information-based approach has failed to provide significant insight into signaling by both primates and other nonhumans" (see also Owings & Morton 1998).

Other learning theorists, such as Tolman (1932), took a different view, arguing that in any conditioning experiment an animal acquires knowledge, and that the animal's behavior "is only an index that a given cognition has been gained" (Gleitman 1991, p. 124). Modern learning theory examines, among many other questions, whether the outcome of a conditioning experiment (the reward) serves simply to reinforce the association between antecedent events or whether the identity of the reward becomes part of the association itself. For example, if rats are trained that a lever press leads to a food pellet and a chain pull leads to sucrose, does the delivery of these rewards simply strengthen the association between certain events ("when in the experimental chamber, press the lever"), or does the reward become part of the "content of learning" (Rescorla 2000), strengthening the associations between the lever and food and between the chain and water? To test between these views, Colwill & Rescorla (1985) selectively devalued either the food or the water. Devaluing the food diminished lever pressing but not chain pulling, whereas devaluing water had the opposite effect. For rats, learning seemed to have included the acquisition of information about the outcome of different behaviors.



**SINGLE PLAYBACK EXPERIMENTS** In their natural habitat, where animals have the opportunity to perform a much wider variety of responses, individuals often react to vocalizations in ways that suggest they have acquired specific information. Vervet monkeys show qualitatively different responses to leopard, eagle, and snake alarm calls (Struhsaker 1967, Seyfarth et al. 1980). Because individuals perform these responses immediately upon hearing a call, without apparently requiring any other supporting information, their behavior strongly suggests that the call has provided them with the information about the presence of a specific predator.

Arguing against this view, Owren & Rendall (2001) draw attention to the fact that vervet alarm calls, like those of many other species, consist of a rapid series of abrupt-onset, broadband pulses with high overall amplitudes: all features designed to evoke an individual's attention and induce arousal. Such vocalizations, they argue, have evolved to "induce nervous-system responses in receivers." They conclude that the notion of information has no "value as a conceptual tool" (2001, p. 61).

There is no doubt that animal alarm calls have acoustic features that may make them attention-getting and arousing. Owren & Rendall (2001) are also correct in noting that these basic characteristics have received too little attention in studies of animal communication, and they offer a reasonable explanation of why call types with different functions, such as alarm calls, distress screams, and more relaxed, within-group vocalizations, take the physical form that they do. The acoustic features of signals are not arbitrary with respect to their function.

Acoustic features alone, however, cannot explain everything. After all, vervet monkeys, suricates, diana monkeys, baboons, and many other species of mammals and birds give acoustically different alarm calls to different classes of predator. All of these alarm call types share many of the same attention-getting, arousing features mentioned above, probably for the reasons that Owren & Rendall (2001) propose. Why, then, are the various alarm calls within each species acoustically so different? Perhaps because, over evolutionary time, natural selection has favored the co-evolution of signalers who warn their kin (Maynard Smith 1965) using different calls for different predators and listeners who recognize the associations between call and referent, thereby acquiring, from each call, the appropriate information.

Upon hearing a vervet monkey's eagle alarm call, nearby animals who are on the ground look up or run into a bush. Animals in a tree look up and/or run down out of the tree and into a bush, and animals already in bushes typically do nothing (Seyfarth et al. 1980, Cheney & Seyfarth 1990a). One could, of course, argue that no information has been acquired and that the eagle alarm call has created in individuals a particular affective state whose effect on behavior differs from one microhabitat to another, thus producing different responses. A more parsimonious explanation, however, posits that calls provide listeners with specific information and that the exact nature of an individual's response to this knowledge varies with his immediate circumstances (Cheney & Seyfarth 1990a).

The reconciliatory grunts of baboons provide another example (Cheney & Seyfarth 1997). Following an aggressive interaction between two female baboons,

dominant individuals occasionally grunt to their victims. To test whether such grunts serve a reconciliatory function, we attempted to mimic reconciliation by playing to the subordinate victim of an aggressive interaction her opponent's grunt in the minutes immediately following the fight. As controls, the same victim heard either no grunt at all or the grunt of another, uninvolved dominant female. Playback of her opponent's grunt affected the victim in several ways. After hearing this grunt, the victim was more likely to approach her opponent and to tolerate her opponent's approach than she was after hearing either no grunt or the grunt of an uninvolved female.

As with alarm calls, one could argue that grunts induce in listeners an affective state that makes them more relaxed and receptive to social interactions. In this case, however, the effect is specific to a particular individual. Playback of her opponent's grunt changes the victim's behavior toward her opponent; playback of an uninvolved female's grunt does not. Any change in the victim's affective state, therefore, is specific to her relations with her opponent. It is also manifested in different ways. If the opponent does not subsequently approach the victim, the victim will. If her opponent does approach, the victim is less likely to move away. The variety of changes in the victim's behavior, each contingent on a different set of circumstances, are most simply explained by positing that the victim has acquired information about her opponent's likely intentions.

As a third example, consider the responses shown by baboons to the sound of an aggressive interaction between two members of their group. In an experiment designed to test whether baboons recognize the calls of other group members and also associate signalers with their close genetic relatives, pairs of unrelated females were played sequences of calls that mimicked a fight between their relatives. As controls, the same females heard sequences that involved either only the more dominant female's relative or neither of the females' relatives. When call sequences involved their relatives, subjects looked towards the speaker for a longer duration than when the sequences involved nonkin. When the sequences involved the other female's relative, they also looked towards that female. Subjects did not look towards one another when call sequences involved nonkin (Cheney & Seyfarth 1999). Taken together, these results argue against the view that responses to vocalizations are fixed and invariant (Wallman 1992). They also contradict the hypothesis that calls have been selected solely to induce specific emotional responses in receivers, because the same call, presented in the same context, elicits different responses in different listeners depending in part on which call it is paired with. As with alarm calls and reconciliatory grunts, the simplest explanation is that calls provide listeners with specific information, and each listener acts on this information depending on her particular circumstances.

The hypothesis that calls act directly on a listener's emotions to change the listener's behavior (Owren & Rendall 1997) and the hypothesis that calls achieve their myriad effects because they provide listeners with specific information are not mutually exclusive. More likely, as Owren & Rendall themselves suggest (1997, 2001), both processes are at work, and vocalizations, together with listeners' memories of past interactions, not only change listeners' affect or

emotion but also provide them with information about predators, social interactions, changes in social relations, or group movements. Indeed, when we eventually arrive at an understanding of the underlying neurobiology, there may be little difference between “emotional calls” that affect emotions and referential calls that affect mental representations.

**A DIFFERENT APPROACH TO THE STUDY OF MEANING** Habituation/dishabituation experiments offer another way to study what is communicated when one animal vocalizes to another. Here the technique (borrowed from research on human infants; see Eimas et al. 1971) is to select two call types from a species’ repertoire and collect baseline data on the responses each normally evokes. Then, in habituation/dishabituation trials, a subject hears call type 1 repeatedly until it has habituated, or until the strength of its response has dropped significantly (different variants of the method, adapted to different field conditions, are not discussed here). Then call type 2 is played. If the subject’s response is significantly below baseline, it is assumed to have judged call types 1 and 2 as similar, at least in the sense that habituation to call type 1 has presumably caused the subject’s weak response to call type 2. By contrast, if the subject’s response to call type 2 is strong and not different from baseline, the subject is assumed to treat the two call types as different, at least in the sense that habituation to type 1 has not affected its response to type 2.

Habituation/dishabituation experiments have two advantages over more conventional, single call playback studies. First, they offer an opportunity to study the criteria by which animals compare vocalizations. When subjects treat two calls as similar (in the sense described above), do they do so because the calls have similar acoustic properties and hence sound alike? Or do they use some other criteria? As already noted, habituation/dishabituation studies have shown that diana monkeys treat conspecific leopard alarms and the growl of a leopard as similar to each other but different from both conspecific eagle alarms and the shriek of an eagle (Zuberbuhler et al. 1999a). Similar experiments have shown that vervet monkey listeners treat intergroup “wrrs” and “chutters” given by the same individual as similar but conspecific female leopard and eagle alarms as different (Cheney & Seyfarth 1988); that rhesus monkeys distinguish kin from nonkin and, within the former class, one individual from another (Rendall et al. 1996); that Barbary macaques (*Macaca sylvanus*) distinguish two types of shrill bark (Fischer 1998); that among three of their putative food calls rhesus monkeys treat “warbles” and “harmonic arches” as similar despite their acoustic differences, but both calls as different from grunts (Hauser 1998); and that baboons learn from experience to distinguish “contact” from “alarm” barks if they are acoustically distinct but not if they are acoustically intermediate (Fischer et al. 2000, 2001b).

In many, but not all, of these cases, subjects treated two calls as similar even though the calls are acoustically different. And whereas we cannot be certain that the animals would agree with our own auditory judgments, often the acoustic difference is striking (Zuberbuhler et al. 1999a). In these circumstances results support the view that listeners process calls at two levels, in a manner analogous to

the different levels of acoustic and semantic processing found in human language. On the acoustic level their response is initially affected by the call's acoustic features, whereas on the semantic level their response is further determined by the information a call provides.

This is not to say that acoustic processing is unimportant, or that the basic physical properties of sound transmission have not played a major role in structuring animal vocalizations. There are now extensive data supporting Morton's (1977) original view that calls given in aggressive circumstances, for example, tend to be low-frequency and noisy, whereas calls in more friendly circumstances tend to be high-frequency and tonal (e.g., August & Anderson 1987; Hauser 1993; Owren & Rendall 1997, 2001). Given that calls may both induce affective responses in listeners and provide them with information, it is this information component of signals with which habituation/dishabituation experiments are concerned.

But what information, exactly? A second goal of habituation/dishabituation experiments has been to approach the study of meaning from a different perspective, by comparing the information conveyed by one signal with the information conveyed by another. At their most optimistic, investigators envisioned a kind of "semantic space" in which some calls would lie close together and be assumed to have similar meanings (because habituation to one produces habituation to the other), whereas other calls would lie far apart and be assumed to have different meanings (because habituation to one did not produce habituation to the other). Ultimately, it was hoped, it might be possible to build a species' dictionary, in which each call type is defined by its relation (synonym, antonym, or somewhere in between) to the others.

This goal, however, has not proved attainable, primarily because few animal vocalizations have the kind of referential specificity found in predator-specific alarm calls. Consider again, for example, baboon grunts. Because baboons' move grunts are given in a relatively narrow set of circumstances, they have the potential to convey quite specific information. Listeners who have just heard a move grunt have probably learned both the identity of the caller and the fact that the group is about to begin, or has already begun, a move. However, infant grunts are less contextually specific. As a result, it is difficult to say what information they provide to listeners other than the identity of the caller and the occurrence of a nonaggressive social interaction.

Many animal vocalizations are more like the infant grunts of baboons than the alarm calls of suricates or vervet monkeys; they are relatively vague in the information they convey to listeners. Does the inability to specify precisely the meaning of an animal's vocalization represent, as Owren (2000) argues, "a basic failure of the information metaphor"? For several reasons we believe it does not.

In language, where the use of sounds to represent features of the environment is no longer in doubt, the question "What do words mean?" is both fundamental and unresolved. As Wittgenstein (1953), Quine (1960), Putnam (1975), and others have argued, it may never be possible to state precisely what an individual means—and what information a listener acquires—when a speaker uses a particular word. Given the difficulty of specifying the meaning of human words, any attempt to

specify the information listeners extract from an animal's vocalization is bound to be even more problematic (Cheney & Seyfarth 1990a, Ch. 5). However, just as the "radical indeterminacy of meaning" (Quine 1960) has not deterred those who study the one-word utterances of children (Fisher & Gleitman 2002) or the confused semantics of neurological patients (Martin 1992) from attempting to determine what a sound means to signaler and recipient, we believe it should not deter those who study the vocalizations of animals from similar research. The inability to specify precisely the information conveyed by a vocalization does not prove that information is entirely absent.

Second, we should not underestimate the rich information that vocalizations can provide to listeners, even when calls are not referentially specific and appear to convey precise information only about the caller's identity. As often noted (e.g., Snowdon 1988), many animal vocalizations are individually distinctive. Beginning with this observation, scientists studying birds, primates, hyenas, and elephants have conducted playback experiments to test hypotheses about individuals' knowledge of their social companions. By using combinations of calls designed to provide listeners with the information that a certain event has taken place (for example, that A and B are involved in a fight, or that D has risen in rank over C), such experiments have shown that birds eavesdrop on singing contests in which they are not themselves involved and subsequently behave differently toward apparent winners and losers (McGregor 2003); that vervets remember which individuals have groomed them in the past and adjust their behavior accordingly (Seyfarth & Cheney 1984); that vervets, rhesus macaques, baboons, hyenas (*Crocuta crocuta*), and elephants (*Loxodonta africana*) recognize the close bonds that exist among matrilineal kin (Cheney & Seyfarth 1980, 1997; Rendall et al. 1996; Holekamp et al. 1999; McComb et al. 2000); and that vervets and baboons recognize others' rank relations (Cheney & Seyfarth 1990a, Cheney et al. 1995b). All of these studies presume that, upon hearing one or a combination of calls, listeners gain at least some information that is extremely precise: information about the identity of the signalers. From this relatively simple starting point animals go on to derive much more complex information about the social events taking place around them, as well as the long-term social relationships these events imply. Contrary to the view that vocalizations have evolved solely to induce affective responses in listeners and that listeners acquire no information from them, these experiments demonstrate that vocalizations do provide nearby "third party" listeners, even predatory bats, with precise information about events. If we grant the acquisition of information to these bystanders, is it logical to deny it to intended recipients?

A third point concerns the future direction of comparative neurobiological research on human and nonhuman species. If we accept the view that information plays little if any role in communication, it follows that the semantic information conveyed by human words is unique, with no parallels in the vocalizations of any nonhuman creatures (Owings & Morton 1998). This conclusion, however, is premature. In fact, we are only beginning to understand the neural mechanisms that allow humans to infer a word's meaning, store it in memory, and compare it with the meaning of other words (e.g., Caplan 1992); the existence of similar mechanisms

in animals is an entirely open issue, now being studied with many different methods, including neuroimaging (Martin 1998). Indeed, one purpose of this review is to draw attention to the many cases in which nonhuman primates respond to vocalizations with behavior that suggests they have processed specific sorts of information. Such ethological work may guide neuroscientists in designing those experiments most likely to reveal both similarities and differences between the neural mechanisms that underlie language and those that underlie communication in other species.

**INFORMATION THAT LISTENERS DO NOT ACQUIRE** Human listeners routinely treat words and phrases not just as semantic representations of objects and events but also as propositions that express the speaker's disposition to think or behave toward those objects in a particular way (e.g., Pinker 1994). By contrast, although nonhuman listeners acquire an extraordinary variety of information from vocal signals, there is little evidence that they also acquire information about the signaler's mental state. Evidence for a lack of mental state attribution by listeners is typically indirect, and comes in two forms. First, in most animal species no systematic observational data indicate that signalers modify their vocal production depending on the mental state of listeners, nor is there any definitive evidence that animals display mental state attribution in any other domain, such as tool use (see above). We therefore assume it is absent in listeners.

Second, in many cases in which we might be tempted to explain the behavior of listeners in terms of mental state attribution, such explanations are usually less persuasive than simpler competing arguments. Consider, for example, the reconciliatory grunts of baboons. If a dominant female grunts to a subordinate following aggression, this changes the subordinate's behavior (Cheney & Seyfarth 1997; see above). One could conclude that the subordinate has recognized a change in the dominant's attitude toward her; that, for example, the dominant is seeking to make her former victim less anxious or afraid. Equally plausible, however, is the likelihood that the subordinate is responding on the basis of a learned contingency. Through experience and perhaps also by observing the interactions of others, she has learned that grunts are correlated with a reduced probability of attack. She therefore tolerates her opponent's approaches and even approaches her opponent with the expectation that her opponent will not attack her again (Cheney & Seyfarth 1996). Functionally, these two explanations are equivalent. The latter, however, does not require a theory of mind. The listener is able to extract subtle and complex information from her opponent's grunt, but this information does not require her also to attribute intentions, motives, or beliefs to her opponent.

These conclusions may not apply to chimpanzees, for which the results of tests for a theory of mind are mixed. For example, there is some evidence that chimpanzees learn more easily than monkeys to recognize the goals and motives of others. Chimpanzees are better than monkeys, for instance, at assuming another individual's role in a cooperative task and at recognizing intentional gestures such as pointing (Povinelli et al. 1990, 1992a,b). They also seem better at emulating

others. When watching a demonstrator use a tool, chimpanzees, unlike monkeys, readily learn the use and function of a tool. However, unlike children, they do not copy the precise motor patterns or methods of the demonstrator (Nagell et al. 1993). As a result, it remains unclear whether the difference in performance between chimpanzees and monkeys stems from chimpanzees' greater capacity to comprehend the goals and intentions of others or from their proficiency in recognizing cause-effect relations (Tomasello et al. 1997, Limongelli et al. 1995, Povinelli & Eddy 1996, Tomasello 1996, Tomasello & Call 1997, Povinelli 2000).

In a far-ranging series of experiments Povinelli (2000) and Povinelli & Eddy (1996) tested whether chimpanzees "appreciate that visual perception subjectively connects organisms to the external world." They argue that to do so the chimpanzees "would have to appreciate that seeing refers to or is 'about' something—in other words, they must interpret seeing as an intentional event" (Povinelli & Eddy 1996, p. 120). Povinelli's evidence argues against such an interpretation. In a typical experiment a chimpanzee was trained to use his natural begging gesture (an outstretched hand) to request food from a human trainer. Then the chimpanzee was given the opportunity to beg from one of two trainers. One trainer was facing the subject and could plainly see him; the other trainer could not because her face was covered (or her eyes were covered, or she was facing in the opposite direction). Given this choice, chimpanzees showed no difference in their preference for one trainer over another. However, 3-year-old children immediately gestured selectively to the person who could see them.

In contrast, other experiments suggest that chimpanzees may have some understanding about the relation between seeing and knowing, even if this understanding is more rudimentary than that of a young child. For example, Tomasello et al. (1998) demonstrated that many nonhuman primates will reliably follow the gaze direction of a human or a member of their own species. Chimpanzees, however, do not simply orient in the appropriate direction and search randomly for something interesting. Instead, they follow gaze direction to a specific geometric location, much as human infants do (Tomasello et al. 1999). More recently, tests by Hare et al. (2000, 2001) suggest that, in at least some situations, chimpanzees know what a conspecific has or has not seen, and from this information may infer what a conspecific does or does not know. Such results do not prove that chimpanzees impute mental states such as ignorance to others or that they recognize that other individuals' visual experiences may be different from their own. They do suggest, however, that some form of a theory of mind may be present in chimpanzees, even if it appears to be absent in other primates.

## SUMMARY

In their natural habitat many animals acquire information from the vocalizations of others. Their acquisition of information has some parallels both with human language learning at the one-word stage and with the information acquired by laboratory animals in conditioning experiments. In other respects, however, the

acquisition of information by animals is governed by fundamentally different mechanisms from those that underlie language.

Natural selection has favored callers who vocalize in ways that change the behavior of listeners and ultimately return benefit to the caller. Simultaneously, selection has favored listeners who detect the links between specific calls and particular events, thereby extracting whatever information may be relevant to them. In many group-living species, where callers and recipients have overlapping reproductive interests, selection has favored callers who give acoustically different vocalizations in different circumstances, thus allowing listeners to acquire more specific information. This information may include, but is not limited to, information about predators or the urgency of a predator's approach, group movements, intergroup interactions, or the identities of individuals involved in social events. In sum, the co-evolution of caller and recipient has favored signalers who call strategically and listeners who acquire information from vocalizations, using this information to represent their environment.

The inability of animals to recognize the mental states of others places important constraints on their communication and distinguishes animal communication most clearly from human language. With the possible exception of chimpanzees, animals cannot represent the mental state of another. As a result, whereas signalers may vocalize to change a listener's behavior, they do not call with the specific goal of informing others or in response to the perception of ignorance in another. Similarly, whereas listeners extract subtle information from vocalizations, this does not include information about the signaler's knowledge. Listeners acquire information from signalers who do not, in the human sense, intend to provide it.

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