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Meaning and Emotion in Animal Vocalizations

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ABSTRACT: Historically, a dichotomy has been drawn between the semantic communication of human language and the apparently emotional calls of animals. Current research paints a more complicated picture. Just as scientists have identified elements of human speech that reflect a speaker's emotions, field experiments have shown that the calls of many animals provide listeners with information about objects and events in the environment. Like human speech, therefore, animal vocalizations simultaneously provide others with information that is both semantic and emotional. In support of this conclusion, we review the results of field experiments on the natural vocalizations of African vervet monkeys, diana monkeys, baboons, and suricates (a South African mongoose). Vervet and diana monkeys give acoustically distinct alarm calls in response to the presence of leopards, eagles, and snakes. Each alarm call type elicits a different, adaptive response from others nearby. Field experiments demonstrate that listeners compare these vocalizations not just according to their acoustic properties but also according to the information they convey. Like monkeys, suricates give acoustically distinct alarm calls in response to different predators. Within each predator class, the calls also differ acoustically according to the signaler's perception of urgency. Like speech, therefore, suricate alarm calls convey both semantic and emotional information. The vocalizations of baboons, like those of many birds and mammals, are individually distinctive. As a result, when one baboon hears a sequence of calls exchanged between two or more individuals, the listener acquires information about social events in its group. Baboons, moreover, are skilled "eavesdroppers:" their response to different call sequences provides evidence of the sophisticated information they acquire from other individuals' vocalizations. Baboon males give loud "wahoo" calls during competitive displays. Like other vocalizations, these highly emotional calls provide listeners with information about the caller's dominance rank, age, and competitive ability. Although animal vocalizations, like human speech, simultaneously encode both semantic and emotional information, they differ from language in at least

one fundamental respect. Although listeners acquire rich information from a caller's vocalization, callers do not, in the human sense, intend to provide it. Listeners acquire information as an inadvertent consequence of signaler behavior.

KEYWORDS: animal communication; language; emotions

INTRODUCTION

In *The Expression of the Emotions in Animals and Man*, Darwin¹ expressed the prevailing views of his time concerning the evolution of animal vocalizations. Like his contemporaries, Darwin believed that the production of sounds by animals other than humans (hereafter "animals") had originally appeared as the involuntary consequence of other bodily movements:

... when the sensorium is strongly excited, the muscles of the body are generally thrown into violent action; and as a consequence, loud sounds are uttered, however silent the animal may generally be, and although the sounds may be of no use [Ref. 1, p. 83].

He noted, however, that over time the production of particular sounds had come to be associated with specific emotions, such as pain, pleasure, or rage, and as a result that many animal vocalizations had come to serve a communicative function. The roaring of lions and the growling of dogs signal these animals' rage and "thereby endeavour to strike terror into their enemies" (Ref. 1, p. 85); the incessant calling of males in the breeding season signals their "anticipation of the strongest pleasure which animals are capable of feeling" and thereby endeavours "to charm or excite the female" (Ref. 1, pp. 84–85).

In the 150 years that followed, Darwin's successors have disagreed about the "voluntary" nature of animal vocalizations but generally accepted his view that the different calls produced by nonhuman creatures are manifestations of emotion and as a result convey information only about the caller's emotional state. For example, Myers² states: "It remains unclear whether the nonhuman primate has developed even rudimentary mechanisms in its brain that can support any voluntary control of its face or voice." After years of field research Goodall³ concluded that "chimpanzee calls are, for the most part, dictated by emotions;" and as recently as 1990 the linguist Bickerton⁴ stated that "...[animal] vocalizations are quite automatic and impossible to suppress." By labeling animal vocalizations as exclusively emotional—in both the proximate causal mechanisms that underlie them and the information they convey—these 19th- and 20th-century scientists drew a sharp distinction between the learned, voluntary sounds that are used in human language and can convey information about external referents and the innate, reflexive sounds that are used in animal communication and can convey information only about the caller's emotions.

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In retrospect, such an either/or dichotomy separating emotional from referential information is difficult to understand. Darwin himself describes many cases in which humans—through their tone of voice, for example—express an emotion like sadness or joy while they are speaking, and as a result simultaneously communicate both referential and emotional information. If the two modes of communication coexist so easily in language, why should the obvious emotional component of animal signaling be taken as proof that the referential component is absent?

Whatever the reason for this long-held bias in interpretation, one conclusion is clear: the emotional nature of animal vocalizations has never been in doubt. From their earliest description by naturalists and explorers, animal screams have been described as “distressful” and interpreted as calls for assistance;¹ their harsh, low-frequency sounds have been described as aggressive and interpreted as signs of imminent attack;⁵ and their clear, high-frequency sounds have been described as submissive and interpreted as attempts to reduce the aggressiveness of opponents.⁵ Given the obvious fact that animal vocalizations both communicate emotions and elicit them in others, contemporary scientists have directed their attention to the more complex question: do they communicate anything else?

AFFECTIVE AND REFERENTIAL COMMUNICATION

Premack⁶ pointed out that there were circumstances in which an affective communication system—even one based entirely on emotion—could effectively become semantic. Suppose, Premack argues, you and I live in a small group and you know that more than anything else I love strawberries. And you also know that more than anything else I hate and fear snakes. Then one day, when I am out of sight behind a bush, you hear me give a great shout of joy. If you really know that I give this call only when I’ve found strawberries and that whenever strawberries are around I can be counted on to make this vocalization, then my cry tells you unambiguously that strawberries are present. Similarly, if you hear a scream and can be certain that I only and always give this call in response to snakes, then my scream tells you without doubt that I have seen a snake. As a result of the listener’s ability to detect a pattern in another’s vocalizing, a system of communication that depends entirely on the expression of emotions has effectively become one that conveys information about objects and events in the world.

The Specificity of Call Production

Was Premack correct? Throughout the animal kingdom, there are many cases in which a vocalization with specific acoustic features is elicited only

by a narrow range of stimuli. Under these conditions, as Premack suggested, calls have the potential to provide listeners with very specific information. For example, the “eagle alarm call” of East African vervet monkeys (*Cercopithecus aethiops*) is elicited almost exclusively by predatory birds, or raptors.⁷ Vervet eagle alarms are rarely given in response to stimuli other than raptors, and raptors 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 type of predator. Through processes that may be similar to Pavlovian conditioning, 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.^{8–10}

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 eagle¹⁰ (Rescorla¹¹ discusses this phenomenon as it applies to Pavlovian conditioning).

The second important variable is the breadth of stimuli that elicit a given call type, defined as the call’s *referential specificity*. Some animal vocalizations are elicited by a broad array of stimuli and thus have a very low referential specificity. Both suricates (*Suricata suricatta*, a South African mongoose shown in FIG. 1) and female diana monkeys (*Cercopithecus diana*) give “alert” calls in response to many stimuli, including mammalian and avian predators, large nonpredatory animals, falling trees, and social disturbances within the group.^{12–14} 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 like the Cape cobra (*Naja nivea*) and to fecal, urine, or hair samples of predators and/or foreign suricates (FIG. 2).¹⁵ Diana monkeys give acoustically distinct alarm calls to mammalian predators like leopards (*Panthera pardus*) and to avian predators like the crowned eagle (*Stephanoetus coronatus*).^{13,16} Such predator-specific alarm calls have a high referential specificity.

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.¹⁰ 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

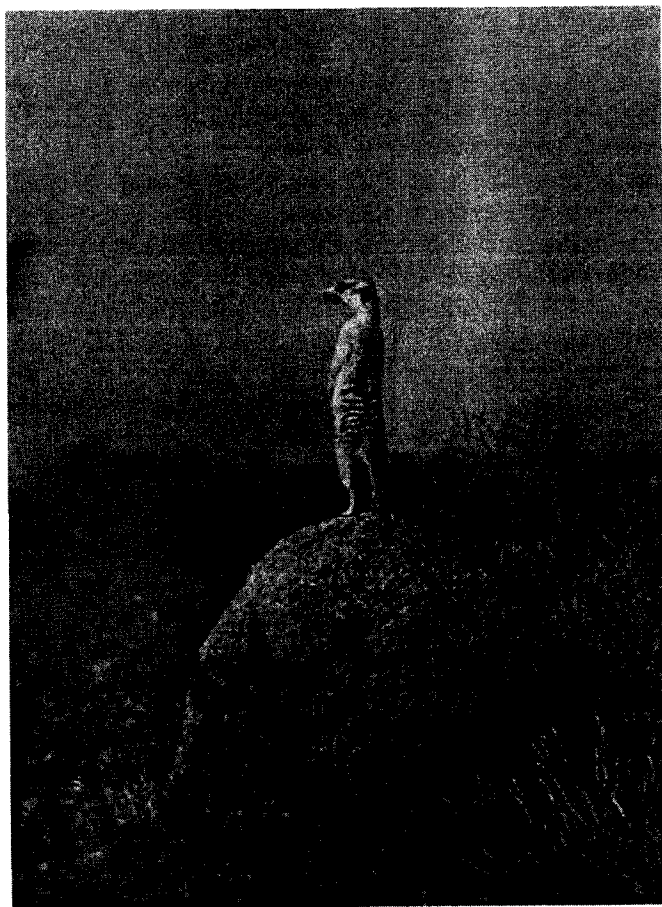


FIGURE 1. A suricate (*Suricata suricatta*) in vigilant posture. Photo by Marta Manser.

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.

Emotional and Referential Communication: Apples and Oranges

As already noted, vocal communication in animals has historically been thought to differ from human language primarily because the former is an

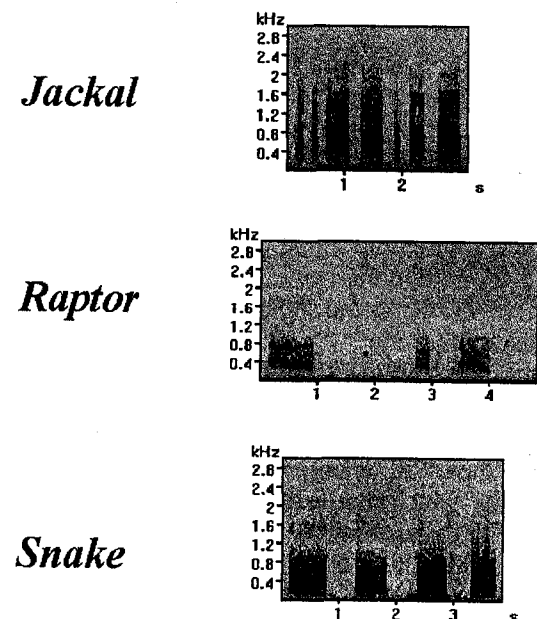


FIGURE 2. Sonograms of alarm calls given by suricates to jackals, raptors, and snakes. In each case, the X axis shows time in seconds; the Y axis shows frequency in kHz.

“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. Following Darwin,¹ many scientists, including Scherer,¹⁷ Bachorowski and Owren,¹⁸ and Bachorowski (this volume) have shown that human speech conveys both referential and emotional information; however, the idea that animal calls might have a referential component remains controversial. Over the past 20 years much ink has been spilled—by ourselves and others—debating whether animal vocalizations could ever provide listeners with information about objects or events other than the vocalizer's emotions and, if so, how referential and affective signaling might interact.^{7,8,19-25} Often the debate has been cast as an either/or opposition between affective and referential signaling. This dichotomy, however, is logically false.

A call's potential to serve as a referential signal depends on the specificity of call production, as defined 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 dif-

ferent mechanisms that lead to this association have no effect on the signal's potential to inform.¹⁰

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 causation 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. Premack⁶ was correct: a shout that is entirely based upon emotion 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. 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.¹⁰ 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.

The grunts of free-ranging baboons (*Papio cynocephalus ursinus*) offer a good example. Baboons live throughout the savanna-woodlands of Africa, in groups of 30–100 individuals that contain adult males, adult females, and immatures. As they forage during the day, the baboons' most common vocalization is a low-amplitude tonal grunt. Though all grunts sound alike to inexperienced human listeners, field observations have shown that grunts in two different social contexts (FIG. 3) can be distinguished by both their mode of delivery and the responses they evoke.^{26,27} *Move* grunts are typically given when the group is about to initiate a move into a new area of its range. They 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 her baby. *Infant* grunts are given in bouts of 5–10 calls and seldom elicit answering grunts from those nearby.^{26,27} Both call

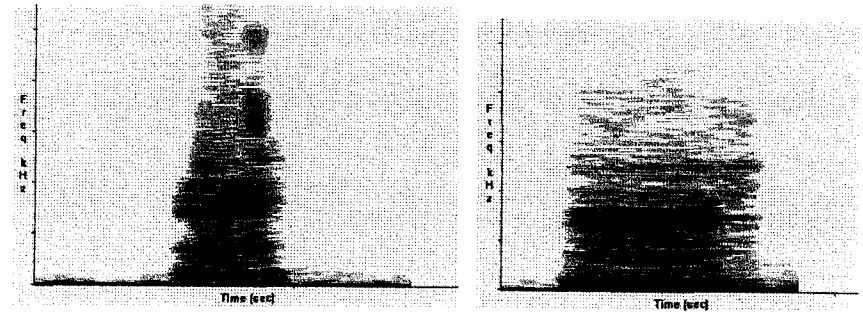


FIGURE 3. Sonograms of representative grunts given by baboons when the group is moving ("move" grunt, left) and when the vocalizer is approaching a mother with infant ("infant" grunt, right). X axis shows time in seconds; Y axis shows frequency in kHz.

types are individually distinctive; although the two grunt types grade acoustically into one another, typical *move* grunts show subtle acoustic differences from typical *infant* grunts.²⁷

Baboons seem to recognize these differences. Playback experiments conducted by Rendall *et al.*²⁸ 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 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.

Should we describe the baboons' grunts as emotional or referential? Rendall²⁹ used behavioral data to code a social interaction involving *move* or *infant* grunts as one with "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 (F0) 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 F0), *infant* grunts were correlated with higher arousal than were *move* grunts. *Infant* grunts also exhibited greater pitch modulation and more vocal "jitter."²⁹ 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^{17,18} (see also Bachorowski, this volume).

It is, of course, difficult to obtain independent measures of an animal's level of arousal under natural conditions. However, similarities between human

and nonhuman primates in the mechanisms of phonation³⁰⁻³² support Rendall's²⁹ conclusion that different levels of arousal play an important role in causing baboons to give acoustically different grunts in the *infant* and *move* contexts. Accepting 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. To understand their potential to act as functionally referential signals, we must consider grunts from a different perspective, that of the recipient.

Baboon grunts vary in their informative value and referential specificity. *Move* grunts, for example, are produced only when the group is moving, about to move, or has just begun a move from one location to another (Ref. 28, personal observation). *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 (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, *infant* grunts have a lower informative value than *move* grunts, for two reasons. First, when listeners hear *infant* grunts, the probability of infant handling is high, but infant handling also occurs in the absence of grunts, when the interacting individuals are silent.²⁶ Second, *infant* grunts are elicited in many contexts other than those that involve infant handling; for example, during friendly interactions between females without infants or as reconciliatory signals after aggression.^{26,33} 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 more than this.

The theoretical perspective outlined here differs from that adopted by Darwin,¹ largely because it examines the vocal communication of animals separately from the perspective of signaler and recipient. As a result, it is open to the possibility that a vocalization whose production is entirely emotional may nonetheless communicate to a listener information that may be described as referential. Further, it is open to the possibility that animal vocalizations may be simultaneously emotional and referential in both their underlying causation and in the information they convey to others. In the sections below we illustrate these last two points with examples from recent research on birds and nonhuman primates. We also discuss their implications for studies of animal cognition.

REFERENTIAL COMMUNICATION AND ITS IMPLICATIONS

From the Signaler's Perspective

Thus far, we have argued that a vocalization can convey referential information to listeners even in cases where the production of calls is a fixed, reflexive reaction on the part of the signaler. We now consider the mechanisms that underlie call production in greater detail.

Is the production of animal vocalizations involuntary? A variety of evidence shows clearly that it is not. In the laboratory, monkeys can learn to give different call types—or to remain silent—under different conditions;³⁴ in the wild, monkeys routinely vary their production of calls depending upon the identity of their social companions,^{35,36} prior events,³⁷ and many other social or ecological factors. Captive songbirds can sing, remain silent, or modify the acoustic features of their song depending on the reward,³⁸ while in the wild many territorial songbirds will "match" the song of a neighbor by replying with the song type from their repertoire that most closely resembles the song type their neighbor just sang.³⁹ The alarm calls of birds, monkeys, and probably many other species may be given or withheld depending on the presence of an "audience."^{8,40}

The existence of multiple alarm call types further weakens the argument that animal calls are involuntary, reflexive signals. When producing different alarms, animals like suricates act as if they classify other species into two broad categories, those that elicit an alarm call and those that do not, and within the former group distinguish between three predator types, presumably on the basis of their physical appearance.

In other species, the classification of predators is more complex and cannot be defined solely on the basis of shared physical features. West African diana monkeys offer a good example. Female diana monkeys 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.¹³ In habituation-disinhibition 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.¹⁶ Male and female diana monkey leopard alarms and the growls of a leopard are very different acoustically, as are male and female eagle alarms and the shriek of an eagle.

Nonetheless, the monkeys treated the three leopard-associated noises and the three eagle-associated noises as if they provided 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.¹⁶ 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. Then, 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.

In this account, the use of terms like *mental representation* and *information* 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. In this interpretation of the mechanisms underlying call production, for example, 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.^{8,16} If this interpretation is correct, it would suggest that emotion and cognition are as inextricably entwined in the production of calls by monkeys as they are in the production of speech by humans.

In summary, if birds, ground squirrels, and monkeys gave only one "general alert" call to all of their predators, their behavior might well be consistent with the kind of uncontrolled, emotional vocalization that Darwin felt was pervasive in the animal kingdom. Clearly, however, it is not. Moreover, to explain the occurrence of acoustically different, predator-specific alarm calls *entirely* in terms of the vocalizer's emotions, we would have to assume that a suricate (for example) experiences a consistently different level of excitement whenever it sees a jackal, an eagle, or a snake and that, over evolutionary time, natural selection has acted in such a way that all suricates now "agree" on precisely what level of excitement (or fear) is associated with each type of predator. Similarly, we would have to assume that all baboons agree on the exact amount of emotion that is associated with a group move as opposed to handling another female's baby.

These assumptions may be true, but they seem unlikely, particularly given several other observations that argue against an interpretation of vocal production as exclusively emotional. We now know that when an animal sees a predator, or suddenly finds itself in a particular social situation, it does not automatically produce a vocalization; instead, in the instant before it calls it acts as if it is taking account of several other factors. What kind of predator is it? Who is nearby? Did I already respond to this same predator a few moments ago? Or, in the case of baboon grunts, what kind of social situation am I in? Who is nearby? How has the listener responded to my calls so far? At present, the most reasonable hypothesis is that vocal production is caused by both the caller's emotions and his assessment of some or all of these other factors. But while we can safely conclude that more than emotions are involved, we cannot yet specify what these other factors are, or precisely how the caller takes them into account.

From the Listener's Perspective

While 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 assess what an individual may have learned only by observing its behavior? Early learning theorists noted that conditioning affects behavior but believed that 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 that the notion of information, or knowledge, was irrelevant.⁴¹ Applied to the study of animal communication, this view finds parallels in Owren's and Rendall's²³ suggestion that "individual primates use vocalizations to produce affective responses in conspecific receivers" (p. 307) and that "the information-based approach has failed to provide significant insight into signaling by both primates and other nonhumans."^{24,42}

Other learning theorists, like Tolman,⁴³ 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."⁴⁴ 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,"⁴⁵ strengthening the associations between the lever and food and between the chain and water? To test between these views, Colwill and Rescorla⁴⁶ 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.

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.^{7,47} Because individuals perform these responses immediately upon hearing a call, apparently without 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 and Rendall⁴⁸ draw attention to the fact that vervet alarm calls, like those of many other species, consist of a rapid series of abrupt-onset, broad-band 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."⁴⁸

There is no doubt that animal alarm calls have acoustic features that may make them attention getting and arousing. Owren and Rendall⁴⁸ 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, like alarm calls, distress screams, and more relaxed, within-group vocalizations, take the physical form that they do (see also Bachorowski, this volume). 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 and Rendall⁴⁸ propose. Why, then, are the various alarm calls with each species acoustically so different? Perhaps because, over evolutionary time, natural selection has favored the coevolution of signalers who warn their kin⁴⁹ 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.^{7,8} 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.⁸

As another 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.⁵⁰ Taken together, these results contradict the hypothesis that calls have been selected solely to induce specific emotional responses in receivers, since 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, 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 behavior²³ and the hypothesis that calls achieve their myriad effects because they provide listeners with specific information are not mutually exclusive. More likely, as Owren and Rendall themselves suggest,^{23,48} both processes are at work, and vocalizations, together with listeners' memory 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.

THE SIMULTANEOUS ENCODING OF EMOTIONAL AND REFERENTIAL INFORMATION BY BOTH SIGNALERS AND RECEIVERS

The preceding sections suggest that emotion and reference are inextricably entwined, both in the production of calls by signalers and in the perception of calls by recipients. Recent work on the vocal communication of suricates (*Suricata suricatta*) directly supports this conclusion.

Suricates are diurnal, cooperatively breeding mongooses that inhabit open semidesert areas in groups of 3 to 33 individuals. They forage for 5 to 8 hours per day, typically at a distance of 20 to 50 m from the nearest burrow or shelter.⁵¹ Foraging animals frequently scan their surroundings for predators. Group members also alternate guarding from a raised sentinel position (FIG. 1).⁵²

Guards and foraging individuals emit several acoustically different alarm calls when they spot a predator. As already noted (FIG. 2), suricates give one alarm call type to mammalian predators, primarily jackals (*Canis mesomelas*) that attack on the ground. When nearby individuals hear this call, they move rapidly toward the nearest system of burrows, looking around vigilantly. Suricates give a second, acoustically distinct alarm to avian predators, primarily martial eagles (*Polemaetus bellicosus*) and tawny eagles (*Aquila rapax*) that attack from the air. When listeners hear a suricate eagle alarm, they freeze and crouch where they are, often scanning the sky. Finally, suricates give a third alarm call type to snakes, such as the Cape cobra (*Naja nivea*) and puff adder (*Bitis arietans*). Their snake alarm call is also given to fecal, urine, or hair samples of predators and/or foreign suricates. Because alarm calls to all of these stimuli cause other animals to approach the caller, give the same alarm calls themselves, and either mob the snake or investigate the deposit, they are collectively termed *recruitment calls*.¹⁵

Manser¹⁵ used discriminant function analysis to classify over 250 alarm calls according to their acoustic features. She confirmed that alarm calls to terrestrial predators, avian predators, and recruitment alarm calls were acoustically distinct (FIG. 4). In addition, within each call class the suricates appeared to give subtly different calls depending upon the imminence of the danger they faced. In any given class, the calls given to a predator that was very close (termed "high-urgency" calls) were acoustically different from those given to the same predator when it was encountered at intermediate distances or far away. The acoustic measures that accounted for variation among alarm call types were, for all but one measure, different from the acoustic measures that accounted for variation within a call type and across levels of urgency.¹⁵ Along the dimension of urgency, changes in acoustic structure were consistent across alarm call types: low urgency calls tended to be clear and more harmonic, while high-urgency calls were harsher and noisier. This difference is illustrated in FIGURE 1, where within each call type the distinction between low- and high-urgency calls represents a shift upwards in discriminant function 1. By contrast, when level of urgency was held constant, there was no consistent rule relating acoustic features to the different predator classes.¹⁵ The referential information about each predator type was not coded acoustically in any consistent way.

In the field, suricates were played alarm calls in the absence of actual predators, and their responses were filmed. Playback of alarm calls given in response to different predators elicited significantly different responses,

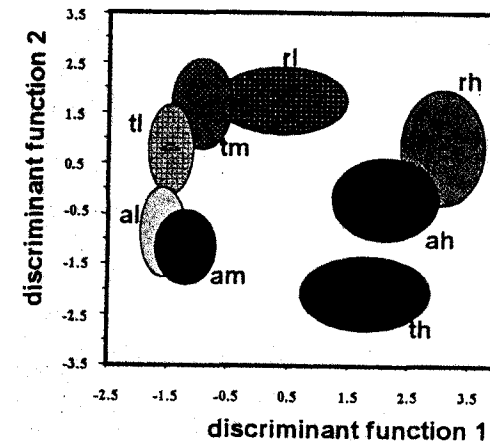


FIGURE 4. Arrangement of the alarm calls given in different predator contexts according to their values as established by discriminant function analysis of the calls' acoustic properties. Ovals are spanned by the mean \pm SD of the first two discriminant functions, with data drawn from 10 runs of the discriminant function analysis. ABBREVIATIONS: t, a, and r stand for terrestrial predator alarms, aerial predator alarms, and recruitment alarms, respectively; l, m, and h stand for low-, medium-, and high-urgency calls, respectively. Reprinted with permission from Manser *et al.*⁵⁴

duplicating behavior seen under natural conditions. In addition to these qualitatively different responses, within each predator class subjects responded in quantitatively different ways to playback of calls that had originally been recorded in circumstances of low, medium, or high urgency. Without blurring the qualitative distinction among responses to different call types, subjects responded most strongly to playback of high-urgency calls, next most strongly to playback of medium-urgency calls, and least strongly to playback of low-urgency calls.⁵³

Suricate alarm calls demonstrate clearly the separate yet intermingled role of emotion and reference in animal communication.⁵⁴ From the caller's perspective, the proximate mechanisms that underlie alarm calls may depend largely upon the caller's emotion. High- and low-urgency calls are certainly correlated with acoustic features known to be associated with fear or anxiety in both animal vocalizations and human speech^{5,17,23,55} (see also Bachorowski, this volume); future research may 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. Alternatively, it may also turn out that suricates' alarms to 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. Regardless of the mechanisms that underlie their production, suricate listeners acquire specific information from the calls they hear—information about specific predators and about the level of danger they represent.

A FUNDAMENTAL DIFFERENCE BETWEEN ANIMAL VOCALIZATIONS AND HUMAN LANGUAGE

To this point, we have argued that emotion and reference interact to affect vocal communication in both animals and humans. There are, however, important limits to this parallel between language and animal vocalizations. The limits arise because most animals—with the possible exception of chimpanzees (*Pan troglodytes*)—cannot attribute mental states to others.^{8,9,56} As a result, while 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 while listeners extract subtle information from vocalizations, they seem not to recognize that signals are reflections of the signaler's knowledge.

Goals and Intentionality in Call Production

Animal vocalizations can be elicited by an extraordinary variety of auditory, visual, or olfactory stimuli.⁵⁷ However, one class of stimuli apparently plays no role in eliciting calls from most nonhuman species. Its absence is interesting, because this class of stimuli 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.⁵⁸⁻⁶⁰ 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.

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.⁶¹

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.^{32,62,63} 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,⁶⁴ there is currently no systematic evidence that knowledgeable individuals ever actively instruct others⁶⁵ or treat ignorant individuals differently from knowledgeable ones.^{10,66}

In marked contrast to humans, therefore, nonhuman primates do not seem to produce vocalizations in response to their perception of another individual's ignorance or need for information (although in the domain of visual communication, evidence of spontaneous, untrained manual gestures by apes that may be intentional does exist; see de Waal, this volume). This is not to say that calls cannot inform; to the contrary, we have already reviewed many cases in which animal listeners obtain information from a vocalization. But such information comes from callers who may not, in the human sense, have intended to provide it. Many animal vocalizations whose production initially seems goal directed are not, in fact, as purposeful as they first appear.

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.⁵⁹ 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; it 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 that it is absent in listeners.

Second, in many cases where 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.³⁷ 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.⁶⁷ Functionally, these two explanations are equivalent. The latter, however, does not require the recognition of another animal's mental state. 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, where the results of tests for a theory of mind are mixed. In a series of experiments, Povinelli⁶⁸ and Povinelli and Eddy⁶⁹ 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."⁶⁹ Povinelli's evidence argues against such an interpretation. In a typical experiment, for example, 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. By contrast, three-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. Tomasello *et al.*⁷⁰ 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.⁷¹ More recently, tests by Hare *et al.*^{72,73} 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 like 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.

CONCLUSION

Since the publication of Darwin's *Expression of Emotions*, there has been little doubt that animal vocalizations reflect the emotions of the caller and that they arouse emotions in listeners. With this observation as their starting point, contemporary scientists have asked whether vocalizations reflect anything more than the emotions of caller and recipient. Specifically, they have asked whether vocalizations convey information to listeners that goes beyond the emotional state of the signaler and whether signalers intend this communication to occur.

Viewed from the signaler's perspective, animal vocalizations are unlikely to be caused exclusively by emotions because they can be given or withheld depending on many different social factors and because—in encounters with different predators, for example—animals give acoustically different calls in situations with similar emotional valence. Field playback studies demonstrate that the alarm calls of at least one mammalian species simultaneously encode information that is both emotional and referential. At present, however, we know relatively little about the precise mechanisms that underlie the production of vocalizations in animals.

Vocalizations that are predictably linked to specific external stimuli or social situations allow listeners to acquire information that is highly specific and that goes beyond information about the signaler's emotional state. In many species, the responses of listeners to different call types suggest hypotheses about the cognitive mechanisms involved and about the ways in which animals classify their social and ecological environment.

While animal vocalizations, like human language, are both emotional and referential in their causation and in the information they convey, they are also fundamentally different from language because, with the possible exception of chimpanzees, animals cannot represent the mental state of another. As a result, while 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, while 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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