
38 Animal Vocal Communication: Say What?

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Researchers interested in animal cognition have sometimes viewed communication as a privileged source of insight into animal minds (Griffin 1976). This view is inspired in large part by analogy to human experience, where language both reflects and affects thought and so provides a window into the workings of our own minds. Not surprisingly, cognitively oriented research in animal vocal communication has also been influenced by other analogies to human language. Without a doubt, the *sine qua non* of language is meaning, communicated via arbitrarily structured words. Proceeding by analogy, researchers in animal communication have thus sought meaning in arbitrarily structured vocalizations, the overarching question being, “*What are they saying?*”

On the one hand, relying on linguistic analogy is perfectly natural. The concept of meaning is certainly familiar to us from language (even if it is sometimes difficult to pin down very precisely) and it makes sense to think that animal vocalizations, like human words, have meaning and are *about* things. On the other hand, this approach is a bit peculiar in that it uses a single, recent, and potentially highly derived system of communication (language) to model scores of other phylogenetically older and evidently simpler systems—thereby inverting scientific common sense. Furthermore, by shoehorning a potentially wide array of communicative phenomena into a single linguistic frame, the approach risks seriously underestimating the diversity of potential mechanisms and functions of animal communication.

For the past few years we have been pursuing a different approach (Owren and Rendall 1997, 2001; Rendall and Owren, in review). In keeping with basic ethological and evolutionary principles, we assume only that the function of communication must ultimately be to influence the behavior of others in ways that are, on average,

beneficial to the signalers (and potentially, although not necessarily, also to the listeners). While such influence may be exerted through a variety of simple mechanisms, none need involve meaning *per se*. Consistent with other features of organismal biology, however, they probably do involve intimate connections between signal structure and function. The approach can perhaps be most simply summarized as emphasizing that it may not be so much *what* is said that matters, but rather *how* it is said, and *who* says it.

A Nonlinguistic Approach to Animal Communication

“How You Say It”—Direct Effects of Vocalizations on Listener Attention and Affect

“It’s not *what* you say but *how* you say it!” The point of this familiar refrain is that information content may be less important than the manner of presentation. This principle is manifest in animal communication in the fact that for many taxa, certain kinds of sounds have direct and marked influences on listener behavior. One extreme but ubiquitous example is the acoustic startle reflex. This involuntary response is particularly triggered by abrupt (i.e., rapid onset) sounds, producing immediate attentional shifts and the interruption of ongoing activity. It also induces a host of basic nervous system responses, including stimulation of reticular formation nuclei in the brainstem that help to regulate overall brain activation. The phenomenon is thought to occur in every hearing species (Eaton 1984), demonstrating that sound can have direct access to low-level nervous-system mechanisms that guide behavior.

Other examples of sounds with direct effects on listener behavior are common. For instance, handlers and herders of various domesticated

animals have long capitalized on the impact of sounds such as whistles, tongue clicks, and lip smacks to manage their charges (McConnell 1991). Here, rapidly repeated pulses and signals with dramatic frequency upsweeps are used to increase motor activity, while smooth, continuous signals with gradual, descending pitch help to decrease activity. Humans themselves are responsive to the same patterns, with frequency upsweeps being used to capture receiver attention and increase arousal in both infant-directed speech (Fernald 1992; Kaplan and Owren 1994; Papousek et al. 1991) and music (Schneider 1963), and arousal-reducing downsweeps having a soothing effect. Additional familiar examples in humans include the effects of fingernails scraping on chalkboards, infant crying, and contagious laughter, all of which have directly noxious or pleasant effects on listeners.

Among nonhuman primates, the taxon with which we are most familiar, numerous vocalizations bear the mark of being designed for similar direct effects. For example, across many species, alarm vocalizations to warn of predators are structurally similar and preserve acoustic features that are well suited to capturing and manipulating attention and arousal in listeners (reviewed in Owren and Rendall 2001; Rendall and Owren, in review). They are typically short, abrupt-onset, broadband calls that elicit immediate orienting responses and movements preparatory to flight. In fact, the same basic alarm call structure is evident in a range of other mammals (Owings and Morton 1998), and also in some birds (Marler 1955), suggesting that the direct acoustic effects on listener attention and affect may be highly conserved, most likely stemming from a function in ancestral vertebrates of identifying and localizing sounds so as to avoid predators and capture prey.

Developmental studies in primates have shown that such generalized startle responses to species' alarm calls are induced even in very young infants in the absence of significant experience with either the calls or predators (e.g., Seyfarth and Cheney

1986; Herzog and Hopf 1983, 1984), as expected from the operation of low-level, brainstem and subcortical structures associated with sound localization, orienting, and autonomic responding. Because attentional and affective systems are the scaffolding for learning, the acoustic properties of these calls most likely specifically facilitate association of the salient dimensions of predator encounters and functionally appropriate escape responses (Rendall and Owren, in review).

Such evolved auditory sensitivities to certain kinds of sound create the opportunity for senders to use vocalizations to engage others, thereby influencing the attention, arousal, and concomitant behavior of listeners in many contexts. Among nonhuman primates, one entire class of vocalizations that we have labeled “squeaks, shrieks, and screams” appears to capitalize on this potential. These sounds are numerous and diverse, and are present in every well-documented primate vocal repertoire, as well as those of many other mammals, birds, and amphibians. They are marked by sharp onsets, dramatic fluctuations in frequency and amplitude, and chaotic spectral structures—exactly the sorts of features that have direct impact on animal nervous systems (Kitko et al. 1999).

Sounds of this type are produced in especially large numbers by younger animals (Owren et al. 1993) and may represent the bulk of their vocal output. In fact, such calls ought to be of greatest value to youngsters, who have little power to influence the behavior of older and larger individuals in other ways. For example, while a frustrated weanling cannot force its mother to permit nursing or close physical contact, it can produce sounds whose acoustic features pick at the mother's attentional mechanisms, increase her arousal state, and with repetition may become quite aversive (Hammerschmidt et al. 1994; Todt 1988). Adults can be similarly impotent, notably when interacting with dominant individuals. Lower-ranking victims of aggression seldom offer much serious physical resistance, whether they are youngsters or adults, but can make

themselves unappealing targets by screaming vociferously, producing loud, jarring bursts of broadband noise and piercing, high-frequency, tonal sounds in highly variable streams whose aversive qualities are difficult to habituate to.

“Who Says It”—Indirect Effects of Vocalizations Mediated Through Social Acuity

A second straightforward but effective way to influence others vocally is simply to advertise one's identity. This strategy is likely to be observed in highly social species where identity has a deterministic influence on the frequency and quality of social interactions. In many nonhuman primates, for instance, individual identity, kinship, and social rank are the pillars of complex social behavior. Who's who and doing what to whom is crucially important, and as a result the animals are attentive to each other's social identity and actions (Cheney et al. 1986).

Vocalizations in these species thus often contain conspicuous cues to caller identity, and listeners are demonstrably responsive to such cues. For example, acoustic analyses have revealed clear identity cues in the “contact” calls used to coordinate activity among dispersed group members in several species (reviewed in Rendall et al. 1998, 2000). For some species, field experiments involving the playback of these calls have confirmed that different group members can be distinguished by voice and that identity cues form the basis for differential responses by listeners (e.g., Mitani 1985; Snowdon and Cleveland 1980; Waser 1977). Among rhesus monkeys, for example, adult females are more responsive to the contact calls of adult female kin than to those of unrelated females in the group (Rendall et al. 1996). In many species, females are also highly responsive to the calls of their infants. For instance, baboon females discriminate the “lost” calls of their own infants from those of other infants and often search anxiously for their own infant if they hear it calling (Rendall et al. 2000).

Conspicuous cues to caller identity are also present in many close-range calls used to mediate face-to-face social interactions (Owren et al. 1993, 1997). Here again, work has confirmed that the identity cues are salient to listeners and influence their behavior. For example, among baboon females, the strongest determinant of listeners' responses to quiet, grunt vocalizations produced in various social contexts is the identity and social rank of the caller. Listeners are far more attentive to the calls of higher-ranking than lower-ranking females (Rendall et al. 1999).

In such face-to-face social interactions, conspicuous vocal cues to identity might seem wholly redundant, given that obvious cues to identity are available visually. However, vocal cues to identity actually have a special capacity to influence behavior in this context because they can be paired with behavioral acts that have significant consequences for others and become predictive of the acts (Owren and Rendall 1997, 2001). For example, in many social species, dominant individuals routinely antagonize more subordinate group members by combining conspicuous threat vocalizations with emotion-inducing aggressive acts such as hitting, biting, and chasing. The significance of the threat calls in predicting attack means that dominant animals can thereafter elicit learned fear and withdrawal from subordinates through the use of the vocalizations alone. Indeed, most conflicts are resolved in exactly this manner, with no aggressive exchange. Identity cues feature centrally here because, given the hierarchically structured social networks of these species, animals will routinely hear many such calls by others over the course of a day without being attacked. Hence, what makes the calls uniquely predictive in any given situation is who produced them.

Depending on one's social potency, then, simply announcing identity can be an effective way to influence others in a range of contexts. In fact, vocalizations are uniquely suited to exerting such influence because they are discrete stimuli that can be readily controlled by the sender and

paired with emotion-inducing behavioral acts. They are also more difficult to ignore than signals in other modalities (simply turning one's head away effectively short-circuits a visual signal, but not a vocal one).

Not all calls are similarly imbued with conspicuous identity cues, however. For example, acoustic analyses and field playback experiments on scream vocalizations produced by victims of aggressive attack show that these calls contain few cues to caller identity (Rendall et al. 1998; Owren 2000). At first, this result might seem surprising because screams have traditionally been assumed to operate over longer distances to recruit aid from genetic relatives who may be out of sight (e.g., Gouzoules et al. 1984). However, in light of the foregoing points, the findings are actually quite sensible. Almost by definition, victims of aggressive attack are socially impotent relative to their attackers, and so their identity is unlikely to influence the balance of power when they are attacked. As a result, the most effective strategy for victims may be to capitalize on the direct effects of sound and be as obnoxious as possible. Loud, hypervariable, noisy screams physically preclude identity cueing, but their aversive properties may motivate attackers to relent, thereby "turning them off" (Owren and Rendall 1997; Rendall 1996; Rendall et al. 1998).

Implications for Mind

The alternative approach to animal vocal communication that we have taken proposes two simple ways in which vocalizations can influence listener behavior in a variety of contexts, and doubtless there are many other similarly simple ways. The two sorts of effects we propose stem directly from basic conditioning principles and in accordance with the widespread relevance of such principles appear to be broadly applicable across numerous types of vocalization and many species of nonhuman primates. In some cases they appear more broadly applicable to other animal taxa and other sensory domains (e.g.,

Endler and Basolo 1998; Ryan 1998). Both effects emphasize the intimacy of the connection between signal structure and function, in contrast to linguistic approaches, which, by analogy to human words, stress the arbitrary nature of signal design. Neither effect recommends use of the linguistic construct of meaning. Thus, vocalizations that serve their function either through direct effects on receiver psychology or through indirect effects mediated by a developed social acuity are not readily interpreted in terms of meaning. To reiterate, the significance of such signals lies not in *what* is said, but rather *who* says it and *how*. Hence, linguistic constructs, like meaning, may have limited application to animal vocalizations.

In fact, recent comparative research on intentionality points to the same conclusion. In human language, the meaning of words stems, not from their sound structure per se, but from the shared conceptual representations they conjure in the minds of speaker and listener alike. Effective communication via shared conceptual representations is made possible by the fact that speakers understand the relation between the words they use and the conceptual representations they instantiate, and they know that others share this understanding. Moreover, they know that others can be informed of phenomena about which they are unaware using words whose representational designata are nevertheless understood. Hence, speech is a deliberate attempt to invoke and sometimes manipulate shared conceptual representations in the minds of others, oftentimes with the goal to inform. The active invocation of such representations, and the sensitivity to others' mental states that is entailed, gives language use in humans the formal property of being intentional (as defined by Dennett 1983). Word meaning, then, is a derivative characteristic of human language that stems from its intentionality.

In contrast, communication in nonhuman primates is not similarly intentional. Recent reviews indicate that even the most cognitively sophisti-

cated nonhuman primates do not use vocalizations as a deliberate attempt to inform others or otherwise modify their mental states (Cheney and Seyfarth 1996, 1998; Seyfarth and Cheney 1997; Rendall and Owren in review). In fact, callers prove to be surprisingly disengaged from their audience, often calling redundantly when all those around them are already aware of a situation, but failing to call in circumstances in which others are unaware of events and could profit from being informed. Evidently they do not appreciate the effect that their calls can have on *what* listeners know. These and additional related findings have led authors to conclude that the proximate cognitive mechanisms underlying human language and nonhuman primate vocal communication are in fact fundamentally different (Cheney and Seyfarth 1996). While the content, or meaning, of human word use hinges on intentional agents—*meaners* to mean what they say—nonhuman primate communication evidently does not. By extension then, we are left to wonder whether there can ever truly be *meaning* in primate vocalizations without there being a *meaner*?

Our response to this question is to suggest that the vocalizations of nonhuman primates (and probably those of many other animal taxa) function differently than the words of human language. Although the animals are clearly capable of forming rich, multidimensional representations of important events, invoking and manipulating such conceptual representations per se is not evidently a central feature of their communication. Instead, the vocalizations of nonhuman primates appear to function primarily through their influence on the affective systems that guide behavior. Note that our emphasis here is on the effect of signals on the affective systems that govern the behavior of receivers, rather than on the affective systems that govern the signal production of signalers, making our approach different in important respects from those of Smith (1977) and others (e.g., Lancaster 1975; Rowell and Hinde 1962).

In accordance with its focus on affective processes, our approach emphasizes subcortical systems like the brainstem and limbic structures that control attention, arousal, and affect, rather than higher-level cortical systems associated with conceptual representation and language comprehension in humans. While research on the neurobiology of vocal communication in primates has long pointed to the central role played by subcortical systems (reviewed in Deacon 1997; Hauser 1996; Jürgens 1998), work outside the laboratory has emphasized higher-level processes, if only by implication, as a result of analogy to human language. However, cortical processing in humans and nonhumans alike is necessarily shaped by the input received from lower-level brain centers. Therefore probing the role that cortically based cognition may play in any communication system depends on first understanding the processing that occurs at subcortical levels. We suggest that actively studying potential effects at these lower levels is likely to contribute to a more solid foundation for understanding the diversity of functions and mechanisms in animal communication, including those that may ultimately result in cortically based processes like the conceptual representations that underlie language use in humans.

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