

Where Is the Information in Animal Communication?

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Abstract

Communication is a central topic in animal behavior studies and yet the dispute over what constitutes communication is far from settled. Over the last few years, a number of papers have revisited the core issues in this field and have advanced divergent views regarding the explanatory power of the concept of “information.” After a review of this debate, an integrative framework is proposed that conceives communication in its elementary form as an interaction between two individuals (sender and receiver) and involves the use of signals by the sender as well as the processing of and responses to those signals by the receiver. Signals are structures or behaviors that have evolved because their effects on other individuals benefit the sender on average, irrespective of whether or not the behavior of the receiver has evolved to be affected. Receivers have been selected to make inferences about the environment, including the behavior of conspecifics. Signals may in this sense be informative to the receiver, because they can be used to assess the state, identity, or subsequent behavior of others. Thus, signals contain “potential information,” which turns into “perceiver information” once processed by a receiver. The value and amount of this information can only be defined from the receiver’s perspective. This framework thus defends the concept of information but rejects the notion that senders have generally been selected to “provide” that information, and that information is “encoded” within a signal. The notion that animals process information also creates a bridge from studies of communication to those assessing the cognitive underpinnings of communicative behavior.

Introduction

Explaining the evolution of communication is a major challenge, and despite many years of research, a number of conceptual issues remain unresolved. This has led to both confusion and sometimes unproductive friction. Some of the disputes appear to stem from diverging initial points in the analyses: some focus on signal evolution, others on responses to signals. Apparently, these different foci have profound implications for the conceptualization of communication. While each approach has its merits as well as shortcomings, the real

challenge is to incorporate insights from both to develop a full understanding of the complexity of communication.

In this chapter, I examine accounts that focus on explaining signal evolution and contrast them with accounts that have been adopted to explain the processing of signals. I review the recent critical discussion of the term “information” in animal communication and argue that this concept should be retained. I believe that the concept of information is indispensable for understanding not only the cognitive mechanisms which underpin the responses to signals, but also the selective pressures operating on receivers.

What Is Communication?

Definitions of communication commonly involve the use of signals and incorporate at least a signaler and a receiver. Notably, in one of the most influential contributions, Maynard Smith and Harper did not even bother to provide a definition of communication in “Animal Signals,” but instead restricted the discussion to the evolution of signals (Maynard Smith and Harper 2003:388). Indeed, the term “communication” is not even indexed in the book. Because a number of researchers who seek to explain the evolution of communication refer to that text, they in turn put more emphasis on the sender’s side than on the receiver’s (Stegmann 2005; Scott-Phillips 2009). Analyses which follow Maynard Smith and Harper’s emphasis on the sender have been labeled “adaptationist,” because they have a strong focus on identifying the selective pressures that shape signal design and affect the costs associated with signaling.

A broad definition was put forward by Todt (1986), who characterized communication as “interactions with signals.” This definition stresses the notion of communication as an integral part of social behavior. Moreover, it facilitates the application of insights from pragmatics, a field in linguistics that has to date only played a minor role in animal communication studies (see Wheeler et al., this volume). One complicating issue in any analysis of communication is that most communicative interactions do not only involve two individuals but rather several subjects, hence the concept of “communication networks” (McGregor and Peake 2000). This is particularly important when different receivers have divergent interests and exert different selective pressures on signalers (Skyrms 2010). For the sake of simplicity, however, this aspect will not be further elaborated here.

What Is a Signal?

An “adaptationist” account seeks to explain the evolution of signaling behavior and the maintenance of honest signaling. Game theoretical models which take into account the costs and benefits associated with signaling are employed

to identify evolutionary stable strategies. Such models have shown that the distribution of interest is crucial for understanding the conditions under which honest signaling can arise. Specifically, when interests diverge, signaling must be costly to maintain honesty. When interests overlap, or when subjects interact repeatedly, cheap signaling may evolve (for an excellent introduction, see Searcy and Nowicki 2005).

Within this framework, there is a strong focus on distinguishing signals from other forms of behavior. Maynard Smith and Harper proposed that signals can be defined as “any act or structure which alters the behavior of other organisms, which evolved because of that effect, and which is effective because the receiver’s response has also evolved” (Maynard Smith and Harper 2003:3). A similar stance was taken by Diggle and colleagues (2007) in a paper that aimed to integrate concepts from animal communication and sociobiology with the phenomenon of quorum sensing observed in bacteria. Quorum sensing is defined as the “accumulation of ‘signaling’ molecules [that] enables a . . . population as a whole [to] make a coordinated response” (Diggle et al. 2007:1245). The term “quorum sensing” has also been invoked to refer more broadly to all phenomena when the behavior of individuals of a social group depends on the number of other individuals performing that behavior (Fischer and Zinner 2011). Diggle and colleagues distinguished between signals, cues, and coercion on the basis of whether or not they had evolved “owing to the effect on the sender” and whether or not it “benefits the receiver to respond” (Diggle et al. 2007:1242)

Scott-Phillips (2008:388) provided an extension of that definition and described signals as “any act or structure that (a) affects the behavior of other organisms, (b) evolved because of those effects, and (c) which is effective because the effect (the response) has evolved to be affected by the act or structure.” Within this framework, signals are distinguished from cues and coercion based on the presence or absence of specific evolution on the signaler’s and receiver’s side, respectively (Table 10.1).

Both accounts assume that for communication to occur, the interests of the signaler and receiver must overlap, otherwise there would be no reason to assume that the receiver’s response evolved “to be affected.” According to this view, the term “signal” is reserved solely for a narrow range of communicative interactions. Whenever interests diverge, these behaviors are defined

Table 10.1 Distinguishing between signals, cues, and coercion within the adaptationist approach to explain the evolution of signaling behavior. Adapted from Scott-Phillips (2008).

	Signaler’s behavior evolved to affect receiver	Receiver’s response evolved to be affected by signaler’s behavior
Signals	+	+
Cue	–	+
Coercion	+	–

as coercion. The advantage of the distinction between signals and coercion is that it stresses the importance of considering the distribution of interests when seeking to explain the evolution of communicative “acts or structures” (Searcy and Nowicki 2005). However, overlap of interest is not a binary variable; instead, it constitutes a continuum ranging from a full overlap to total divergence. The degree of overlap of interest may vary in relation to the coefficient of relatedness, for instance, but also the cost functions associated with responding. An example is found within the realm of parent-offspring conflict, where the overlap of interest changes continuously over time. Imagine a needy youngster who expresses hunger or distress. Early on, caretakers benefit from investing in their offspring and respond immediately with nurturing behavior. However, at some point in time, it becomes more beneficial for the parent to invest in further offspring, creating a conflict (Trivers 1974). In nonhuman primates, such conflicts are often accompanied by tantrums and long bouts of screaming and wailing. Although mothers will initially give in to such attempts to reestablish contact and nurse, they will eventually behave aggressively toward the infant until the youngster gives up (“weaning conflict”). If one adopted the definition provided in Table 10.1, one would need a criterion to decide when the communicative behavior (screaming) turns from a signal to coercion. Because the structure of the behavior may even stay constant, while only the receiver’s response changes, I believe that the distinction between signal and coercion is not helpful. In the following, I will therefore adopt a broader definition and use the term “signal” for all acts or structures that have evolved for the purpose of altering the receiver’s behavior—irrespective of whether or not the receiver’s behavior has also evolved for that purpose. Furthermore, the adaptationist approach does not do justice to the receiver’s contribution to the equation. Tellingly, a wording such as “receiver’s response evolved *to be affected* by signaler’s behavior” [italics mine] carries the connotation that the receiver is a passive receptacle, unable to evolve its own strategies. It has long been known that this is not the case (Krebs and Dawkins 1984).

What Is Information?

A large body of research in animal communication is implicitly or explicitly based on the assumption that communication can be characterized as the transfer of information from the signaler to the receiver (reviewed in Rendall et al. 2009). The concept of information transmission was adapted from information theory. Although information theory was initially developed to study the processes of message encryption and their subsequent retrieval in technical systems (Shannon and Weaver 1949), it quickly found its way into communication studies. A number of authors have pointed out that such a concept is misleading because signalers do not benefit from “providing information,” at least not when interests diverge. Instead, the argument goes that the senders

benefit from influencing others to behave in a way that is in their own interest (Dawkins and Krebs 1978; Rendall et al. 2009). Moreover, it is questionable whether information can be determined independently from the receiver, calling into question not only the concept of information transmission, but also that of information content of a signal. Thus, it is argued that the concept of information is useful as a by-product, at best (Scott-Phillips 2008), or not at all (Rendall et al. 2009). Others have taken a more balanced view (Scarantino 2010) or have attempted to defend the concept of information (Seyfarth et al. 2010; Wheeler et al., this volume).

A critical view of the informational stance is not particularly novel. Dawkins and Krebs, for example, argued that “it is probably better to abandon the concept of information transfer altogether” (Dawkins and Krebs 1978:309; cf. Krebs and Dawkins 1984). However, in the subsequent edition of the same textbook, their view became more nuanced, casting the evolution of communication as an interplay between mind reading and manipulation, thus giving credit to both roles commonly invoked in communication (Krebs and Dawkins 1984).

As a number of authors have pointed out, one drawback of information theory is that it is agnostic with regard to the semantic aspects of signaling. Thus, it is not suited to capture the content of communication (Scarantino 2010). Indeed, the mathematical theory of information centers on the general statistical properties of the environment, whereas biological systems will only respond to statistical variation that has fitness consequences for them (i.e., that is related to conditions and events meaningful to the individual). This is the fundamental difference between Shannon information and biological information. One important insight from information theory, however, is that signals may undergo potential changes during transmission. This view has highlighted the selective pressure that different habitats may have on signal design; another valuable insight is the importance of noise. More importantly, the *conception* of information as a reduction of uncertainty to the receiver has proven to be useful. Thus, information theory offers some useful insights for understanding the receiver’s behavior, because it connects communication to learning theory. Although it is difficult to provide exact quantifications of the information content of a given signal, Skyrms suggested that “the natural way to measure the information in a signal is to measure the extent that the use of that particular signal changes probabilities” (Skyrms 2010:8).

As Krebs and Dawkins (1984) wrote, any animal could benefit if it could behave as if predicting the future behavior of other animals in its world, or, as Humphrey put it, animals are “nature’s psychologists” (cf. Krebs and Dawkins 1984:387). Thus, the question is whether animals can use signals (or cues, for that matter) to predict subsequent behaviors and upcoming events. There is ample evidence that this is the case. Learning theory offers tools to analyze and predict how animals form associations between stimuli, stimuli and responses, as well as behaviors and outcomes of these behaviors.

Consider threat signals. The evolution of threat signals (and display signals) can be explained on the grounds of an assumption that it benefits both the signaler and the receiver to avoid the costs of fighting. Both parties of an interacting dyad should attempt to resolve conflicts at the lowest possible cost; for instance, by using signals that communicate the signaler's intent or that reflect the signaler's quality. Because interests typically diverge in such situations, it pays for the receiver to distinguish between honest or reliable signals and unreliable ones.

For the present purposes, whether a given signal reliably predicts a certain action is of particular interest. If a receiver has been threatened by a higher-ranking animal, but chooses to stay anyway, and has subsequently been attacked, it will most likely learn that threat signals predict aggression. This view mirrors that put forward by Krebs and Dawkins (1984): they proposed that signalers should benefit from paying attention to other animal's intentions. Here, "intention" is used loosely without reference to the mental state of the animals, and it does not imply that the animal intends to communicate its intentions. Likewise, animals can learn that the occurrence of alarm calls predicts the appearance of a predator (this falls into the category of environmental information *sensu* Krebs and Dawkins 1984). Signals can be viewed as informative because they have the potential to reduce the uncertainty about what will happen next. Because animals benefit from ceasing to respond to unreliable (or uninformative) signals, one can make clear predictions under which circumstances animals learn to ignore specific signals. The same is true for indexical signals that are related to sender properties, such as size or hormonal state. It is important to stress that whether or not a signal reduces uncertainty can only be determined from the receiver's perspective and depends on the context of occurrence, previous experience, preceding signals, and so forth.

Skyrms distinguished between the informational content of a signal and the quantity of information in a signal. He suggested that "the informational content of a signal consists in how the signal affects probabilities," while the "quantity of information in a signal is measured by how far it moves probabilities" (Skyrms 2010:34).¹ Variation in structures or behaviors that allows receivers to predict upcoming events, gauge the quality of a sender, or detect changes in the environment has the potential to provide information as well. It is not trivial to distinguish between signals and other classes of behaviors. For instance, "walking" is part of locomotion. "Walking toward another animal,"

¹ Skyrms (2010:34) goes on to explain this as follows: "It is easy to see the difference. Suppose, for instance, that there are two states, initially equiprobable. Suppose that signal A moves the probabilities to 9/10 for state 1 and 1/10 for state 2, and that signal B moves the probabilities in exactly the opposite way: 1/10 for state 1 and 9/10 for state 2. Even without knowing exactly how we are going to measure quantity of information, we know by considerations of symmetry that these two signals contain the same amount of information. They move the initial probabilities by the same amount. But they do not have the same information content, because they move the initial probabilities in different directions."

however, may also be a signal of dominance. Likewise, looking in a particular direction provide the animal with information about what is going on in that area. In nonhuman primates, eye gaze provides an important cue (Teufel et al. 2010); looking *at* some other animal may indicate that an approach or an attack will follow. A third example is the clearing of the throat, which may indicate a cold or signal the intent to begin a speech. Thus, some behaviors function as a signal, although the form or structure was not specifically selected for communicative purposes.

At the same time, one needs to be aware that all sorts of other variation in the environment (“data”) have the potential to be informative. Therefore, signals constitute only a small subclass of the data that organisms are selected to process. For instance, it has been shown that animals respond adaptively to changes in acoustic signals that can be used to gauge signaler distance, such as effects due to reverberation. In fact, Rendall et al. (2009:237) noted that “perceivers have evolved sensory systems to detect, localize and discriminate *important features* of the environment” [italics mine]. I suggest that the “important features” might as well be termed “potential information.” What is important can only be determined from the signaler’s point of view; hence replacing “information” with “important features” does not provide a more accurate insight into animal communication than the application of the concept of information.

In the very strict sense, therefore, communication does not consist of information transmission, and signals do not contain information. Instead, information is generated by the receiver. Accordingly, statistical regularities in the environment are potentially informative, and signals contain *potential* information. Once this is clarified, however, I argue in favor of a mildly relaxed use of the terminology. For instance, I think it is acceptable to say in shorthand that information transmission has occurred once a signal has been intercepted by a receiver. Likewise, signals can be characterized in terms of their information content, in the sense that a researcher might be interested in studying, for instance, the association between signal variation and some physiological variable, as long as it is understood that this is only potential information.

Message and Meaning

The notion that communication entails the encoding of information on the sender’s side and its decoding on the receiver’s side has also been criticized because of its supposed implicit symbolic connotation (Scarantino 2010). Yet, some terminology is needed to describe the process of how, for instance, signaler features are related to signal features. Although frequently correlational, there is now ample evidence that in the acoustic domain, specific aspects of the call vary with signaler fighting ability, body size, and hormonal state (Fischer and Zinner 2011). To circumvent the connotation of symbolic communication,

one might prefer to avoid the phrase that “information has been encoded.” However, whenever there is variation in signal structure in relation to subsequent behavior, sender quality, or changes in the environment, one might say that this pattern constitutes “potential information.” This is equivalent to the distinction between message and meaning (Seyfarth and Cheney 2003a). The message is thus the variation in signal structure (or usage) that is related to some aspect of the signaler or the context of signaling. The meaning is generated by the receiver, who processes and interprets the signal, and chooses the appropriate response in light of all the available evidence (i.e., contextual cues).

On conceptual grounds, it is important to distinguish between meaning and responses. In principle, the meaning could be defined as the information the receiver obtains from the signal, in the sense that a signal has been associated with a particular context, the emotional state of the signaler, or some change in behavior. Empirically, however, the meaning can only be inferred from the responses, and therefore, responses and meaning have often been (in my view incorrectly) conflated. Smith (1977), for instance, proposed that signals attain meaning by a combined assessment of signal features and the context in which they are given, but I suggest that it is more accurate to say that the responses are chosen on the basis of signal information as well as contextual information. In other words, the decision rule takes in the occurrence or variation in a signal, as well as variation in context. For instance, vervet monkey responses to acoustic signals have been shown to vary with call type (“alarm call”) as well as sender identity (Cheney and Seyfarth 1988). That is, listeners process who is calling, and they may vary their responses in relation to signaler reliability. The amount of information extracted in terms of identifying the caller remains the same. At the same time, the same signal may elicit quite distinct responses, depending on the context in which it occurs. Although it has not been demonstrated experimentally, it is conceivable that receivers are able to classify a call as belonging to a certain category (“alarm call”) while varying their response in relation to context (“no predator in sight” vs. “a lion right in front of me”). This issue warrants further investigation.

It has been argued that studies of (nonhuman primate) acoustic communication should consider the influence that specific acoustic properties have on broadly conserved sensory and affective systems in listeners (Owren and Rendall 2001; Rendall et al. 2009). It is certainly true that sharp onsets may elicit startle responses. Likewise, it seems plausible that most nonhuman primates would respond to aversive loud and noisy screams with avoidance responses. The diversity of alarm calls in different species, such as growls, barks, twitters and hoots, however, rejects a simplistic explanation. Given that nonhuman primate vocalizations are largely innate, it is not surprising that the same broad call types may be used in different contexts (Fischer et al. 2004). Therefore, multiple selective pressures, including those related to function, as well as evolutionary constraints must be taken into account when trying to link signal structure to function. Furthermore, nonhuman primates quickly learn to

pay attention to the alarm calls of other species, such as the whistles and snorts of antelope, the calls of birds, or the growls of leopards. Even more strikingly, animals may respond to the absence of a signal, such as in the “watchman’s song” found in meerkats, *Suricata suricatta*, where sentinels on guard regularly emit soft sounds. If they cease vocalizing, this signals danger to their conspecifics (Manser 1999). Clearly, such a behavior cannot be reduced to a simple physiological response.

Referential Signaling

Rendall and colleagues (2009:233) lamented that “animal communication studies often use analogies to human language.” While this is perhaps true for the study of nonhuman primate signaling, most researchers studying olfactory communication in moths, the roaring of red deer, or electric communication in fish would probably disagree. The question really is: What do we gain and/or lose by applying linguistic concepts?

Obviously, any attempt to identify the evolutionary roots of the human language faculty (Hauser et al. 2002) will need to begin with a definition of the features that are seen as characteristic of language or speech. While largely resulting in a failure to find equivalents of the human language faculty (at least at the side of the signaler), one must concede that the linguistic approach was necessary to reach that insight. We would not know that nonhuman primate calls fail to fulfill the criteria for symbolic or iconic communication, if it were not for the adaption of a semiotic and/or linguistic stance. Given the deep human desire to make sense of the origin of language, I predict that this branch of research will expand further, and the quest is now to understand the suite of changes that occurred during evolution, which eventually allowed early humans to speak (Fischer and Hammerschmidt 2011). Such studies of nonhuman primate communication need to be complemented by other studies that are more ecologically grounded, or which look at other selective pressures that shape communication today.

One core concept in those studies that investigated which (if any) aspects of nonhuman primate signaling behavior may be linked to aspects of the human language faculty is the topic of referential signaling. The diagnostics for referential signaling are production specificity on the side of the sender and differential responses on the side of the listener (Macedonia and Evans 1993; Seyfarth and Cheney 2003b). The latter are indispensable to infer whether or not animals attribute differential “meaning” to the sounds (but see discussion above). Production specificity is frequently inferred by comparing signals that are given in different contexts; if these reveal systematic acoustic variation, it is assumed that the criterion of production specificity is met. However, production specificity can only truly be assessed if the vocalizations given in *all* contexts are sampled and compared. Obviously, production specificity tends to be

overestimated when only a few selected contexts are included in an analysis. What does it tell us, however, if and when production or context specificity can be diagnosed? Initial accounts favored a view according to which the animals “denote” the predator type, for instance, or possibly the appropriate response, akin to a proposition. I would argue that we still have limited insights into the cognitive operations underlying the usage of calls in different contexts. In most of the cases where context-specific calls are found, the most parsimonious explanation is that variation in calls that allow listeners to select the appropriate response constitutes a selective advantage that leads to the evolution of increasingly different vocalizations. In other cases, variation may be related to changes in hormone levels or arousal. Whenever the variation is sufficiently systematic, listeners can make inferences about ongoing or upcoming events and adjust their behavior accordingly, despite the fact that in the strict sense, these calls do not refer to anything at all.

Another issue in this realm is that signals can be placed on a referential-to-motivational continuum. Scarantino (2010:E3) noted that “the notion of a continuum makes theoretical sense only on the condition that approaching one end entails moving away from the other.” He argued that no such trade-offs exist. I do not believe, however, that this is the problem. First, Marler and colleagues (1992) conceived the referential-to-motivational continuum as variation along two different dimensions. Thus, in principle, a signal could show no variation in relation to external referents, but substantial variation in relation to motivation.

My main criticism of the “motivational-to-referential” continuum is of a different sort; namely, it sets up a false dichotomy. “Motivational” change can also be “functionally referential.” Consider the case of rhesus monkey screams that vary in relation to the dominance of the aggressor (Gouzoules et al. 1984), and let us assume that this leads to different degrees of aversion, which in turn causes the animals to produce calls that vary in terms of noise. This is a clear case of a change in the signal in relation to motivation. A receiver may now be able to infer that animal X has been attacked by a high- or low-ranking individual. In this sense, the signal now functions referentially. In other words, “motivation” refers to signal production, whereas “referentiality” refers to the receiver’s ability to understand the link between signal structure and occurrence, or context, or some other variable. Given that nonhuman primates and the majority of other terrestrial mammals have little volitional control over the structure of their vocalizations (reviewed in Hammerschmidt and Fischer 2008), it is safe to assume that the production of all acoustic signals is largely motivational. Todt (1986) distinguished between three components of the internal state: an affective one representing the animal’s evaluation of the situation; a motivational one related to the tendency to exhibit a given behavior; and an arousal component related to the propensity to respond to incoming sensory information and the immediacy of a given response. This idea is closely related to the proposal that responses, particularly to predators, may vary in relation

to predator class but also to the imminence of the danger (response urgency). At present, it is difficult to determine whether the sight of different predators, for instance, leads to changes in affect and/or motivation (probably both). In the framework of explaining acoustic variation, I suggest that the referential-to-motivational continuum be abandoned. It may be more illuminating to test whether such a three-dimensional construct as the one presented above provides a useful framework to understand variation in nonhuman primate signals. It might also provide a conceptual link to studies that seek to explain variation in the expression of emotion in the human voice.

Conclusion

In the strict sense, information can only be defined from the receivers' perspective, because statistical regularities in the environment are only turned into information by the receiver. Statistical regularities in the environment should thus be conceived as potential information, whose value and content depends on the state of the receiver. Communication consists of the use of specific structures or behaviors that have evolved because they affect the behavior of others, as well as the processing of these signals by the receiver. Communication can only be understood at the ultimate and proximate level if the interdependence between signaler and receiver is considered.

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