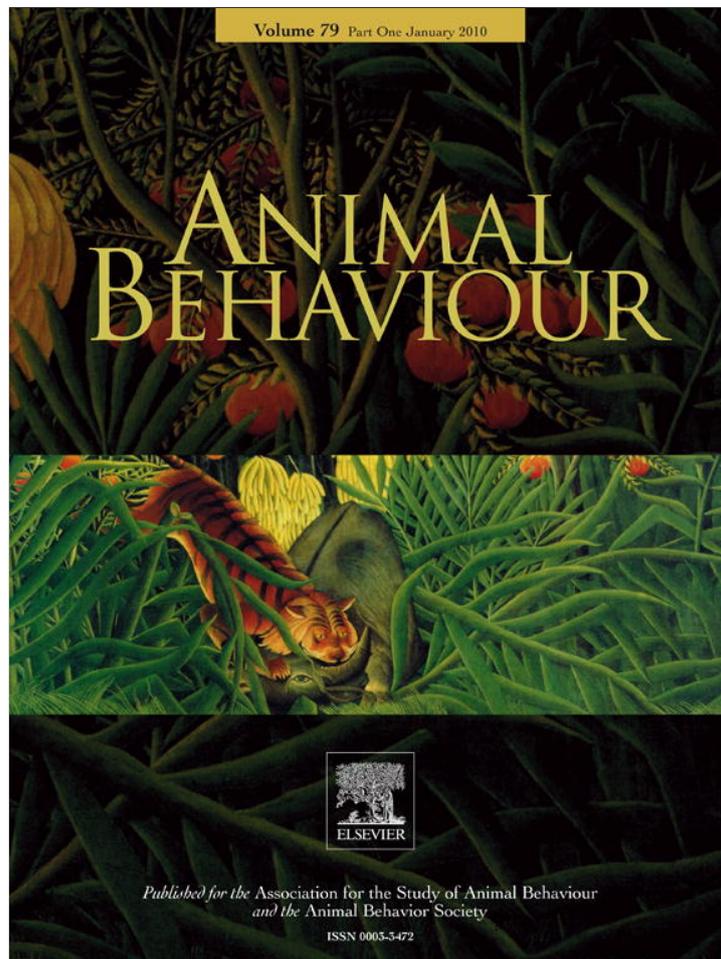


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Animal communication: insights from linguistic pragmatics

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What do animal signals mean? Rendall et al. (2009) recently argued that such a question is in fact ill posed. To accept the question as meaningful (no pun intended) depends, according to Rendall et al., upon the adoption of the conduit metaphor (Reddy 1979), in which information is seen as a concrete entity that is to be passed from signaller to receiver. Certainly, this idea has intuitive appeal, and it pervades the everyday language of communication (e.g. 'get your message across'; 'send me your ideas', etc., see Reddy 1979). As Rendall et al. observed, this perspective necessarily adopts (sometimes explicitly, sometimes not) the Shannon and Weaver model of communication (Shannon & Weaver 1949), in which messages are encoded, transmitted, and then decoded. Yet this is, according to Rendall et al., an inappropriate way in which to characterize animal communication. They suggest instead that animal communication is better considered as a process of *influencing* other organisms. Rendall et al. argued for this on the grounds that the conduit metaphor overlooks many important factors that shape signal design, including that it fails to capture the asymmetries between signaller and receiver that are an inherent part of communication.

Rendall et al.'s reasoning is persuasive. However, they did not mention the most compelling argument in their favour: that influencing others is actually what it means to communicate (Maynard Smith & Harper 2003; Scott-Phillips 2008). Furthermore, any information transfer that does occur (in the sense that uncertainty is reduced, Shannon & Weaver 1949) is entirely dependent on what the animals are *doing* to one another (Scott-Phillips 2008). For example, when a vervet monkey, *Chlorocebus aethiops*, hears the alarm call for an eagle, uncertainty is reduced not just with respect to the presence or otherwise of an eagle, but also all of the following: that there is another member of its troop in the local vicinity; that the caller's productive tools (its vocal tract, etc.) are in working order; that the monkey's own receptive tools (its ears, etc.) are in working order; and so on. In fact, the amount of information contained in the signal is infinite: there are an infinite number of ways in which the world could change such that the vervet would no longer hear the alarm call in a normal way (an earthquake may occur; a meteor may hit the vervet; the laws of physics may suddenly change; and so on). Uncertainty about all of these events is reduced by the fact that the vervet has heard the alarm call in a normal way, meaning that an infinite amount of information is 'transferred'. The difference between these events and the presence of the eagle is that the alarm call evolved to reduce uncertainty about the presence of eagles, but it did not evolve to reduce uncertainty about the other possibilities. Similarly, the vervet's response (hiding in bushes) is an evolved reaction to the call. All of which means that even if we do wish to conceive of communication

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in terms of information transfer then we must also say what the information is for. (There is an analogous problem in the philosophy of language (Quine 1960), and also in artificial intelligence, where it goes by the name of the frame problem (McCarthy & Hayes 1969).)

Consequently, any model of communication must take account of the functionality that underpins communicative behaviour, both productive and receptive. Information transmission is then derivative of this; it is a property that emerges from communicative interactions (Hauser 1996). We can say what and how much information is transferred, but only after we have specified the functions of both the signal and the response. It is thus this functionality, and not information, that is the foundation of communication. We are thus led to a definition of signals as acts (or structures) that cause an effect in another organism, evolved to cause such an effect, and that are effective because the reaction is also evolved (Maynard Smith & Harper 2003; Scott-Phillips 2008). Signals may on occasion fail to achieve the effect they are designed for; but when they are successful we may term the interaction communicative. This account is crisp, and successfully captures the various scenarios we would *prima facie* wish to term communicative (Stegmann 2005; Scott-Phillips 2008). Furthermore, its symmetrical nature (both signal and response must be adapted) reflects the fundamentally interactive nature of communication. This definition, in which signals are behaviours that are designed to have effects, clearly accords with the emphasis that Rendall et al. placed on communication as a process by which animals influence rather than inform one another. It also provides the foundation for a general account of communication (de Sousa 2008).

Where does this leave Rendall et al.'s central question: the meaning of animal signals? Rendall et al. asked the question rhetorically, since they explicitly rejected the adoption of linguistic description in the analysis of animal communication. However, it would be a mistake to reject all linguistic constructs. Pragmatics is the subdiscipline of linguistics that addresses how the external environment affects language. For example, the same utterance can mean different things depending on the context in which it is produced ('it's raining' could mean any of 'get the umbrella', 'I don't want to go out after all', 'the harvest will be better this year', and so on). Broadly speaking, semantics is concerned with meaning in isolation, while pragmatics deals with meaning in context (Carnap 1958). There is, then, a natural epistemic connection between pragmatics and the evolutionary study of animal communication: both are concerned with how external influences shape behaviour in general, and signal design in particular. In the case of animal communication, those external influences are the evolutionary pressures that give rise to both productive and receptive communicative behaviours; in the case of pragmatics, those external influences are the context in which communication occurs. Not all linguistics shares this perspective; Chomskian generative grammar, for example, explicitly argues that the external environment is strictly irrelevant to linguistic form (e.g. Chomsky 1975, 1988; see also Lakoff 1991).

There should, then, be insights from pragmatics that can inform the study of animal communication. I will highlight three: (1) that pragmatics has developed an account of meaning that is inherently functional, and hence a consilient account of meaning can be developed; (2) that, consistent with Rendall et al.'s emphasis on influencing rather than informing, pragmatics often thinks of utterances as tools for *doing* things to the world; and (3) that a central distinction in pragmatics, between communicative intent and informative intent, can help distinguish between reliability and honesty, two terms that have previously been used synonymously in the animal communication literature.

The first point, then, is that while much linguistics (e.g. formal semantics; see Cann et al. 2009) typically defines meaning in a denotative way, as a relationship between an utterance and the phenomenon it refers to in the world, pragmatics offers an alternative approach that can form the basis for a more consilient approach to meaning. Within pragmatics, meaning is typically defined as an intention on the part of the speaker (see Grice 1975). As such, it is cast in terms of proximate mechanisms, which explains why meaning is often put in quotes marks when we refer to the 'meaning' of animal signals, as it is clearly not applicable to other species, where the functional goals of communication will be achieved with different mechanisms. However, the definition of communication given above opens up the possibility of a more general notion, one that operates at the functional level of explanation. Since all signals, by this definition, have functions, then that function can be considered an integral feature of the signal. For example, the ultimate function of the honeybee dance is to improve the foraging efficiency of other workers (and thus ultimately improve the dancer's inclusive fitness); and the ultimate function of a vervet alarm call is to cause avoidance behaviour in other vervets. If meaning is understood in these functional terms, rather than as a proximate mechanism, then the correct response to Rendall et al.'s rhetorical question 'do vervet alarm calls *mean* 'leopard', 'large cat', 'run into a tree'?' (2009, page 236, italics in original) is the latter of these, since that is the effect that the signal has been selected to induce. Similarly, the ultimate function of human utterances is to produce behavioural changes in their listeners (mostly via changes in their internal representations of the world), a consilient account that accords with pragmatic approaches to language, which emphasizes meaning as an intention on the part of the speaker to have such effects on their listeners.

The second point is that much pragmatics already thinks of communication as a matter of influence rather than information. If any one idea can be said to lie at the heart of pragmatics, it is the thesis of linguistic underdeterminacy (Carston 2002; Recanati 2004; Atlas 2005). The literal meaning of an utterance and the meaning that the speaker intends to communicate are often (and in fact are necessarily) different. In sarcastic utterances, for example, the literal meaning is the direct opposite of the intended meaning. As such, utterances cannot be taken to specify the speaker's meaning fully. This observation does not sit well with the informational view of communication, in which a signal's meaning is fully specified if we have access to both the message itself and an algorithm with which to decode it. Pragmatics has thus developed an alternative to the Shannon and Weaver model of communication, one based on the production and interpretation of evidence for the intended speaker's meaning (see e.g. Sperber & Wilson 1995). On this view, communication is not so much about encoding and decoding as it is about ostension (the act of providing evidence for the meaning you intend to communicate) and inference (the act of using that evidence to converge upon the intended speaker's meaning). Utterance production is then straightforwardly seen as an act that is designed to induce others to change their representations of the world in some way (a mechanistic description that maps directly onto the functional account given above). Indeed, one of the seminal books in pragmatic theory is entitled *How To Do Things With Words* (Austin 1962), with the emphasis very much on the *do*. This is clearly consistent with Rendall et al.'s argument that animal communication should be considered more as a matter of influencing rather than informing.

A third insight from pragmatics that can inform matters of evolutionary concern is the distinction made between informative and communicative intent (Grice 1975; Sperber & Wilson 1995). Informative intent is, predictably, a speaker's intention that the listener understand the content of the produced stimulus.

However, before this can occur, the listener must recognize that the speaker has an informative intent; that is, that the stimulus is a communicative behaviour at all. A speaker's communicative intent, then, is the intention that the listener recognize that the speaker has an informative intention in the first place. This distinction is important because it highlights that there are two separate dependencies in any communication system: one to do with whether listeners recognize that a signal is being produced at all (if they do not then no communication can occur); another to do with whether it is worthwhile for listeners to attend to the signal (if they do not, then the system will collapse).

Cast in evolutionary terms, the second of these is the classic problem of animal signalling theory, that of honesty: how do signals remain honest in the face of the evolutionary pressure to defect? There are several possible answers to this question, including handicaps, indices, repeated interactions and others (reviewed in Maynard Smith & Harper 2003; Searcy & Nowicki 2007). The first dependency is, in a sense, more fundamental: how do actions and reactions become calibrated to each other such that they become signals and responses? From an adaptive perspective, the question is a trivial one: there is no incentive for signallers to use signals that are unknown to the intended audience. However, from a phylogenetic perspective the matter is far from trivial, for essentially the same reason: how can a signal evolve if there are not already listeners that will respond to it? There are two classic answers: ritualization (Tinbergen 1952; Lorenz 1965; Huxley 1966) and sensory bias (Ryan 1990; Bradbury & Vehrencamp 1998). In ritualization, cues are exapted for a communicative purpose. An example is the use of urine (and/or faeces) to mark territorial boundaries. Many mammals relieve themselves when they experience extreme fear, which may occur as they leave the safe environment of their own territory. If so, then conspecifics could use the presence of urine as a guide to the area within which the focal animal feels safe. The urine would thus be a cue. However, there is now a pressure for the focal animal to urinate so as to inform the conspecific that this is their natural territory, even when they are not fearful. If this happens, then urine is being used as a signal. In sensory bias, coercive behaviours are exapted for communicative purposes. For example, female birds may search preferentially for red when foraging, because they only see red on certain seeds that are good for them. A male that adds red to its plumage may be able to exploit this preference and thus gain more mating opportunities (see e.g. Bradbury & Vehrencamp 1998). This is coercion. However, if that coercion affects the female positively then she may evolve a more enhanced or nuanced preference for red, precisely so that she mates with males with red plumage. If so, then the red plumage is now a signal.

The distinction between informative and communicative dependencies allows us to distinguish between two terms that have previously been used synonymously in the animal communication literature: honesty and reliability. Honesty refers to the informative dependency, reliability to the communicative dependency. The difference is most clearly illustrated in the case of human language (Fig. 1; this perhaps partially explains why much work in evolutionary linguistics (e.g. Galantucci 2005; Scott-Phillips et al. 2009) is concerned with the question of how interlocutors can agree on the meanings of words, with relatively little focus on the question of evolutionary stability). However, it also applies to animal signalling in general: we must explain both how mutually dependent signals and responses can evolve (communicative dependency) and how they remain stable (informative dependency). Consider again the use of urine to mark territorial boundaries, and the corresponding response of some rival animal not to encroach upon the territory. First, we must ask why urination is

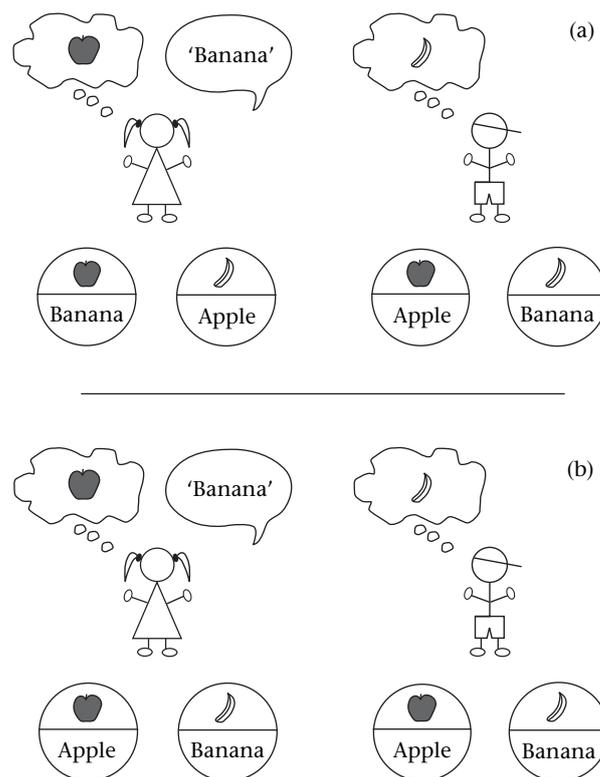


Figure 1. The twin problems of (a) reliability and (b) honesty. In both cases the girl has said 'banana' having thought of an apple, and this fails to correspond to the boy's mapping of the sound (which is as per the convention in English). However, the reasons for this failure are different in each case. In (a) the girl has a different (in fact, the precise opposite) mapping from sounds to meaning than the boy, and this makes her unreliable. In (b) she has the same mappings as the boy but has chosen to communicate a different meaning than the one she has thought of, and this makes her dishonest.

paired with nonencroachment, rather than with some other behaviour (and, indeed, why nonencroachment is paired with urination and not some other stimulus): why is urination not associated with, say, sexual attraction? As discussed above, the answer lies in phylogeny of the behaviours, as catalogued by the process of ritualization. Similarly, the reason that we use the linguistic conventions that we do (such as the fact that 'banana' is associated with a certain type of yellow fruit) rather than some other conventions (for example, we could use 'apple' to refer to the yellow fruit) is inherently historical (Lewis 1960): once the convention is established, no individual has an incentive to use the words differently. Second, we must ask what keeps the association stable: why do signallers not urinate around much larger territories? Here, also as discussed above, the answer lies in the

Table 1
The two separate dependencies in communication

Dependency	Gloss	Corresponding evolutionary problem
Communicative	How do signals and responses become calibrated to each other?	Reliability
Informative	What maintains the evolutionary stability of signals?	Honesty

Linguistic pragmatics emphasizes the difference between communicative and informative intent. Informative intent is the intention that listeners understand the content of an utterance; communicative intent the intention that listeners recognize that there is an informative intent (see main text for discussion). This distinction can be used to separate out two ways in which signals and responses are mutually dependent upon each other. Each poses a separate evolutionary problem.

study of the evolutionary stability of communicative behaviour, that is, in the various selection pressures that prevent the evolution of dishonest behaviour. The distinction between these two orthogonal issues is summarized in Table 1.

This clarity with respect to the different types of dependencies that exist within a communicative interaction illustrates how pragmatics can be a potentially rich source of insight for the study of animal communication. It follows two other conceptual points that both accord with Rendall et al. (2009)'s emphasis on communication as a matter of influence rather than information: first, that the pragmatic approach to meaning straightforwardly maps onto an account of communication predicated on biological function; and second that, consistent with this, pragmatics typically thinks of utterances as tools that do things to listeners, rather than as pieces of information. More generally, although typically described in terms of mechanisms (specifically human intentions), pragmatics offers an approach to meaning (and linguistic communication more generally) that is predicated on the ends to which language is used. This means that it shares with evolutionary approaches to animal communication a concern with how the external environment can influence (communicative) behaviour. It is thus expected that the two fields can become more closely integrated with one another. That integration will proceed further if a consilient conception of communication can be agreed. Rendall et al.'s (2009) arguments that we should reject the conduit metaphor as the basis for communication are to be embraced, not only for the reasons they give, but also because it paves the way for the development of such an account. There will most likely be practical reasons to consider communication in informational terms (for example, when an animal's behaviour depends upon the integration of several different communicative stimuli). However, that does not mean that information is what is basic to communication. It is instead derivative of a functional account. This vision of communication as a matter of influencing others captures the fundamentally interactive nature of communication, and consequently lies at the very heart of what it means to communicate.

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