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Forum

Animal communication between information and influence

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Rendall et al. (2009; henceforth, ROR) have offered a sombre diagnosis of the state of the information concept in the animal communication literature. In a nutshell, they have argued that it is woefully imprecise, covertly misleading in its implicit assumptions, and in some cases plainly incoherent. Their recommended therapy is to get rid of the information construct all together. Questions such as 'What information do animal signals convey?', they conclude, are 'ill-posed' (Rendall et al. 2009, page 238). As an alternative, they offer an account of animal communication in terms of influence. I agree (in part) with the diagnosis, but not with the therapy. If a bad information construct stands in the way of progress, so does its wholesale elimination. I argue that we can address ROR's worries while preserving a theoretically useful notion of information, thereby combining the insights of information-based and influence-based approaches into a richer hybrid.

INFORMATION AND IMPRECISION

Let us consider the problem of imprecision first. ROR point out that animal communication researchers often speak of information loosely and metaphorically, without explicitly stating what they mean by it. On other occasions, researchers make a knee-jerk appeal to Shannon's (1948) theory of information, and suggest that it can provide a theoretical foundation for information talk in animal communication. ROR lament this state of affairs, and I agree with them completely. The costs of loose and metaphorical information talk are clear. First, problematic assumptions may be injected into the discussion through the backdoor and drive theoretical choices without having been critically considered. Second, in the absence of a clear account of information, cross-purpose talk lurks at every corner. Different researchers may mean different things when they speak of information. As a result, terminological disputes risk being confusedly mixed with substantive disagreements on the nature of animal communication.

Knee-jerk appeals to Shannon's (1948) theory of information are also problematic, because Shannon's theory is programmatically disinterested in the semantic problem of communication, which concerns what signals mean or carry information about. (ROR use the notions of 'information' and 'meaning' interchangeably throughout their paper, and I follow this practice here.) What interested Shannon was the engineering problem of communication, which concerns the efficient reproduction of symbols across noisy physical channels (e.g. the efficient reproduction of a conversation across phone lines).

Shannon's notion of information measures the degree to which the selection of one of a set of possible symbols is surprising: the

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more surprising a selection is, the more Shannon information it generates. What the symbols selected mean or carry information about, if anything, has no bearing on the amount of Shannon information they generate.

I conclude with ROR that animal communication theorists should neither rely on informal usage nor try to squeeze into Shannon's theory a semantic story. From this it does not follow, however, that we would be better off without the information construct. What follows is simply that, if animal communication theorists want to use information for theoretical purposes, they should provide a rigorous theory of information that successfully addresses the semantic problem of communication.

INFORMATION AND LANGUAGE

ROR's case against information relies mostly on the conviction that information-based (and meaning-based) metaphors have misleading connotations because they implicitly suggest that animal signals should be understood on the model of linguistic signals. Since there are key differences between linguistic and nonlinguistic signals, 'informational approaches often either overlook, obscure or underspecify many of the fundamental properties of signal phenomena' (Rendall et al. 2009, page 234). ROR have described linguistic signals as being characterized by three main features absent in animal signals: arbitrariness, theory of mind capacities and encoding.

First, ROR claim that linguistic signals are arbitrary vehicles with respect to the information they carry. Several alternative sequences of symbols can be equally successful at conveying the same information. It is an arbitrary fact resulting from linguistic convention that the sequence 'an eagle is coming' carries the information that an eagle is coming rather than, say, the information that water is boiling. ROR argue that animal signals are not similarly arbitrary, in the sense that they are structurally designed to engage the attention of their recipients against competing stimuli and background noise, and to bring about specific behaviours and/or motivational states upon reception.

Courtship calls, for instance, have evolved to allow recipients to locate senders in competition with one another and have the ability to influence directly the neuroendocrine processes that regulate the sexual receptivity of female recipients (Wilczynski & Chu 2001). Alarm calls tend to be 'short with abrupt onsets and broadband noisy spectra', and they can directly produce 'orienting responses and movements preparatory to flight' (Rendall et al. 2009, page 236).

Second, in order for the information carried by a sentence to be exchanged, a complicated network of communicative intentions grounded in theory of mind capacities has to be in place between utterer and hearer. ROR argue that, on the contrary, nonhuman animals 'show little of the perspective taking and mental state attribution abilities' characteristic of human language (Rendall et al. 2009, page 235; cf. Penn & Povinelli 2007).

They suggest that the mechanisms of signal production are affective in nature, and that they are 'modulated primarily by involuntary processes involving subcortical brain structures such as the limbic system, midbrain and brainstem' (Rendall et al. 2009, page 235). As they point out, this constitutes an important disanalogy with language, in that language production crucially relies on volitionally controlled neural processes in temporal and frontal-lobe cortical regions (Lieberman 2002).

Third, animal communication theorists routinely refer to 'encoding' and 'decoding' operations as being part and parcel of the communicative process. At a first approximation, encoding and decoding are coordinated mapping operations from one set of symbols to another set of symbols. In successful linguistic communication, a sender 'encodes' a meaning, for example that an eagle is coming, into a sentence, the sentence reaches a recipient, and the recipient 'decodes' the original meaning from the sentence. ROR argue that this conduit metaphor, as Reddy (1979) first labelled it, does not apply to animal signals.

They point out that in the case of sentences there is 'representational parity' between senders and receivers, which 'occurs when the speaker and the listener have similar representational processes that ensure corresponding coding and decoding of signal meaning' (Rendall et al. 2009, page 235). But this sort of representational parity presupposes a web of interconnected communicative intentions that demands cognitive capacities beyond the reach of nonhuman animals. Moreover, ROR suggest that the information carried by animal signals is not 'encoded' in the signal in the sense that it is 'fixed' into it independently of signaller and receiver. Their suggestion, tantalizing but not fully developed, is that signaller and/or receiver play in animal communication a more active role than simply encoding and decoding a commodity that exists independently of them.

The differences between linguistic and animal signals highlighted by ROR are real and important. My point is that they are not grounds for rejecting the notions of information (and meaning) altogether. Rather, these differences indicate that an account of information suitable for animal communication should not conceive of animal signals as structurally arbitrary, presuppose theory of mind capacities for their senders or receivers or think of information as being 'encoded' in animal signals the way it is in sentences. Plenty of theories of information can in principle satisfy these requirements.

INFORMATION AND FUNCTIONAL REFERENCE

ROR reserve their most scathing criticism for the construct of functional reference: they argue that it is 'incoherent'. The influential notion of functional reference aims to preserve the idea that animal signals convey information/meaning while acknowledging their differences from linguistic signals. It can be defined as follows (Seyfarth et al. 1980; Marler et al. 1992; Evans 1997, 2002): X functionally refers to Y when (1) X is reliably elicited by Y (production criterion) and (2) X's presentation reliably leads to responses adaptive for dealing with Y (perception criterion).

Let us consider these two criteria in turn. First, 'referential signals should exhibit a degree of stimulus specificity' to what they refer to, which is to say that 'eliciting stimuli must belong to a common category…although the size of this category…could vary considerably' (Macedonia & Evans 1993, page 179). For example, an alarm call could in principle be reliably elicited by 'red-tailed hawks', a fairly narrow category, or by 'dark flying objects', a much broader category.

Second, 'referential signals should be sufficient, in the absence of the eliciting stimulus and of other normally available cues, to allow receivers to select appropriate responses' (Macedonia & Evans 1993, page 180). The proviso that other cues are not available is meant to ensure that the signal X itself is causally responsible for the selection of responses, rather than being responsible in combination with other contextual factors (e.g. the nonvocal behaviour of the signaller).

Vervet monkey, *Chlorocebus aethiops*, alarm calls are a paradigmatic example of functionally referential animal signals. As first argued by Struhsaker (1967), vervet alarm calls are specific to three classes of predators: leopards, eagles and snakes. If so, the production condition for functional reference is satisfied. Moreover, receivers of alarm calls in the wild reliably produce adaptive behaviours. Receivers of leopard calls run into trees, receivers of eagle calls run out of trees, and receivers of snake calls stand up tall.

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Seyfarth et al. (1980) demonstrated that such adaptive behaviours are also produced in the absence of the relevant predators, for instance when recordings of alarm calls are played in the absence of any contextual cues. If so, the perception criterion of functional reference is also satisfied.

Referential signalling has been documented with respect to several species, including nonhuman primates (e.g. Hauser & Marler 1993; Di Bitetti 2003), birds (e.g. Evans & Marler 1995; Bugnyar et al. 2001), suricates, *Suricata suricatta* (e.g. Manser et al. 2001) and honeybees, *Apis mellifera* (e.g. von Frisch 1974; Gould & Gould 1988).

Holders of the theory of functional reference conclude that animal signals often mean, or carry information about, their functional referents. At the same time, it is acknowledged that a great many animal signals are not functionally referential. Some signals are described as 'purely motivational', as in the case of the distress and contentment calls of precocial birds and human infants. These signals are thought to be driven by internal motivational states such as hunger, pleasure and pain, and to be largely independent of the characteristics of the external stimuli present when they are elicited.

However, functional reference theorists such as Marler et al. (1992) propose that a dichotomous separation between referential and motivational signals must be rejected. What they suggest instead is that animal signals fall on a continuum between an 'ideal' motivational case, where 'signal structure will approach independence from specific [external] stimulus characteristics' and an ideal 'referential' case, where signal structure 'is wholly dependent on [external] stimulus characteristics and is unaffected by variation in motivational state' (Marler et al. 1992, pp. 70–71). Most 'and perhaps all signals', they conclude, 'have both referential and motivational components' (Marler et al. 1992, page 71).

Does the notion of functional reference provide an account of information and meaning suitable for animal signals? ROR are convinced that it does not. First, they claim that the very notion of functional reference amounts to a 'conceptual retreat', in that 'it represents an admission that the central, linguistically based concept of meaning simply does not apply' (Rendall et al. 2009, page 236). But this is exactly the kind of retreat we need, because any theory of information and meaning suitable to make sense of animal signals, as ROR themselves have argued, should not confuse animal signals with linguistic signals. So this admission is an insight of functional reference theorists, rather than a shortcoming of their research programme.

Second, ROR are convinced that further evidence of the 'logical incoherence' (Rendall et al. 2009, page 236) of the notion of functional reference is revealed by the attendant idea that animal signals lie on a continuum between a purely motivational end and a purely referential end. Their point, as I understand it, is that signals that reliably reflect variation in motivational states can nevertheless functionally refer to external stimuli because they can be reliably associated with the external stimuli that caused such motivational states to change in the first place (more on this below).

If this is so, then either the 'continuum evaporates', or 'any given signal must be said to exist at multiple locations on the continuum' (Rendall et al. 2009, page 236), namely as both motivational (if we focus on the producer) and referential (if we focus on the receiver). Since both options are deemed unpalatable, ROR conclude that the construct of functional reference is plagued by 'conceptual and empirical ambiguities' (Rendall et al. 2009, page 236). Attempts to preserve its scientific integrity despite these ambiguities 'risk shoehorning an increasing array of fundamentally incompatible signalling phenomena into a narrow, linguistically inspired informational frame' (Rendall et al. 2009, page 236).

I agree with ROR that the continuum idea is conceptually confused. But it does not follow that the notion of functional reference is itself incoherent: there is no such thing as guilt by conceptual association. The trouble with the continuum idea is that it confuses two issues we should keep separate: how signals are produced, and what information, if any, they carry. Proponents of functional reference often present the hypothesis that calls are produced by primarily motivational states as an alternative to the hypothesis that they functionally refer to external stimuli.

For instance, Macedonia & Evans (1993, page 178) wrote that, instead of referring to external stimuli, a vervet monkey 'vocalization could, for example, be a manifestation of the fear or panic associated with the threat of predation. Alternatively, it could reflect a desire for the dispersal or aggregation of group members'. But whether the vocalization is produced through fear or a desire for dispersal or yet another mechanism has no bearing at all on whether it refers to an external stimulus. What has a bearing is only whether the call is reliably elicited by such a stimulus, and whether it reliably leads to responses adaptive to that stimulus when the call, but not the stimulus, is present.

Functional reference theorists do acknowledge that animal signals can in principle functionally refer to things other than external events, such as the affective state of the signaller or the species to which it belongs or its reproductive qualities or its subsequent behaviour (Marler et al. 1992). This is in part why they reject the view that signals are either motivational or referential, claiming that they lie on a continuum between purely motivational and purely referential ends.

The problem is that they still buy into the continuum idea. The notion of a continuum makes theoretical sense only on the condition that approaching one end entails moving away from the other. But no such trade-off exists: signals do not have to buy referentiality at the price of motivational grounding, nor motivational grounding at the price of referentiality.

One sense in which approaching the motivational end does not correspond to moving away from the referential end is that signals can in principle functionally refer to internal motivational states, provided that the production and perception criteria are satisfied for them. Another sense in which approaching the motivational end does not correspond to moving away from the referential end is that an effective strategy to functionally refer to external stimuli is to have classes of internal motivational states track classes of external stimuli.

When this is the case, the signal may acquire functional reference to external stimuli by means of being elicited by internal motivational states that reliably correlate with them. It may well be that leopard calls are elicited because vervet monkeys faced by leopards experience a particular kind of fear that leads them to generate a leopard alarm call. This is fully compatible with, rather than alternative to, the thesis that leopard calls functionally refer to leopards.

So what are we to make of the conceptual confusions afflicting the notion of a continuum between motivational and referential ends? For ROR, such confusions are sufficient grounds to dismiss the construct of functional reference altogether. But this would amount to throwing away the baby with the bathwater. The bathwater is the idea that animal signals lie on a motivational-to-referential continuum. I propose we throw it away. The baby is the idea that animal signals have the ability to be functionally referential. I propose we keep it, because it allows us to make sense of the behaviours of signal recipients.

There is no better explanation for why receivers of leopard calls run into trees, receivers of eagle calls run out of trees, and receivers of snake calls stand up tall than the fact that such alarm calls functionally refer to distinct classes of predators. It of course an

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open empirical question whether any particular signal is functionally referential, and to what extent functional reference is a widespread phenomenon in animal signalling. What I have argued is simply that, once separated from the motivational-to-referential continuum idea, the notion of functional reference is both perfectly coherent and insightful.

SIGNALS AS CARRIERS OF NATURAL INFORMATION

I have argued so far that ROR's analysis fails to establish that questions such as 'What do animal signals mean?' or 'What information do they convey?' are 'ill-posed' questions, namely questions we should not be asking. On the other hand, ROR have made a convincing case that we will not be able to answer such questions successfully if we think of animal signals carrying information and meaning the way sentences do. In this final section I explain why we do not have to conceive of information and meaning that way.

Grice (1957) distinguished between a non-natural and a natural sense of the word 'meaning'. When we say that three rings on the bell of the bus mean that the bus is full, or when we say that the sentence 'an eagle is coming' means that an eagle is coming, we are using the word 'meaning' in its non-natural sense. On the other hand, when we say that smoke means fire, or that spots (on the face) mean measles, we are using the word 'meaning' in its natural sense. Grice's terminological distinction between two types of meaning can be extended to a distinction between two types of information: natural information and non-natural information (see Piccinini & Scarantino, in press).

The fundamental difference between non-natural information and natural information, that is, between the two senses of the word 'meaning', is that the former, unlike the latter, can fail. Three rings on the bell of the bus and the sentence 'an eagle is coming' carry non-natural information: that the bus is full and that an eagle is coming. If three rings go off when the bus is empty, they still carry non-natural information about the bus being full. Similarly, if I say 'an eagle is coming' when it is not, my sentence still carries non-natural information that an eagle is coming.

Natural information, on the other hand, cannot similarly fail. Smoke carries natural information about fire, and spots carry natural information about measles, by virtue of the fact that there exist in nature reliable correlations between these types of events. If reliable correlations between smoke and fire and spots and measles were to stop existing, smoke would stop carrying natural information about fire and spots would stop carrying natural information about measles altogether. Natural information is grounded in reliable correlations between types of events in the world.

ROR's central worry can now be restated as follows: animal signals are often wrongly assumed to be carriers of the sort of non-natural information sentences carry. Since animal signals differ from sentences in a number of important respects, ROR conclude that we should stop asking what information and meaning animal signals carry, and focus on investigating what influence they have. On the picture they recommend, animal communication is fundamentally a signaller's attempt to affect the behaviour of a recipient in ways that are advantageous to the signaller.

But there is an obvious alternative, which is to think of animal signals as carriers of natural information the way smoke is a carrier of natural information, and incorporate this notion of information into an influence-based approach. (There is also the option of distinguishing varieties of non-natural information distinct from the non-natural information carried by sentences. I disregard this aspect in what follows.) None of the worries raised by ROR directly apply to the notion of signals as carriers of natural information. Natural information can be made precise, it is coherent, and it is not problematically influenced by the linguistic model, but rather defined in opposition to it (Dretske 1981; Piccinini & Scarantino, in press; Scarantino & Piccinini, in press).

The main reason why we should try to incorporate the notion of natural information into an influence-based approach is that one of the most effective ways for a signaller to influence a recipient is to provide him or her with natural information. Consider the difference between the influence exerted by a courtship call that only prepares a recipient for sexual activity through direct stimulation of the nervous system and a courtship call that both prepares a recipient for sexual activity and carries the natural information that the sender is a high-quality male (it is an open empirical question whether courtship signals manage to carry such information by reliably correlating with reproductive quality). This sort of natural information may explain why a particular high-quality male reaps the benefits of the recipient's state of sexual arousal when multiple males issue courtship calls at the same time.

So while it is true that we will not fully understand signalling if we only focus on the information signals carry, it is also true that we will not fully understand signalling if we only focus on the recipient-oriented physical properties of signals by virtue of which signals directly influence recipients. We may not even fully understand why signals have the recipient-oriented physical properties they do without understanding what they functionally refer to (if anything). For instance, the task of referring to one's reproductive quality, the task of referring to predators and the task of referring to food appear to provide signal senders with three importantly different design problems.

The ecumenical conclusion I have come to is that information-based and influence-based approaches should not be contrasted, but rather combined in a cooperative venture for mutual advantage.

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