

Commentaries

We agree that what signals *do* is primary, and talk of information can serve this stance in several ways (cf. Horn, 1997). Here are three. First, signals only *do* things on average, so talk of information helps us to articulate the best case (normative/selected-for) scenario. Second, because the effect of the signal itself is only one piece of the puzzle of how it *does* things (the rest being context), talk of information helps us articulate what piece the signal contributes (that's what semantics is). Third, if information is inherent in particular manifestations of the physical world (e.g. sight of prey) that, when they are signals, are evolved behaviours of other animals, then surely the clearest shorthand (*not* metaphor) for speaking of both influences in a unified way is to talk of information.

Horn, A. G. (1997). Speech acts and animal signals. In D. W. Owings, M. D. Beecher & N. Thompson, eds., *Communication. Perspectives in Ethology*, Vol. 12. New York: Plenum Press, pp. 347–358.

Andrew Horn and Peter McGregor

Communication without perceiver adaptation. Scott-Phillips and Kirby adopt a pragmatic approach to the information construct, emphasising information as correlations between signals and objects or events in the world. We concur with this view, while noting that such regularity exists whether or not anyone attends to it. As elaborated in our commentary on Scarantino's contribution, a conceptual firewall is therefore needed between information as correlations in the world and observer representations of those correlations. In defining signalling and communication, Scott-Phillips and Kirby require both that signallers be specialised to influence perceiver behaviour and that perceivers be specialised to be so influenced. Thus, the authors argue that an interaction is merely coercive if an actor relies on its own physical power to influence the behaviour of another. In contrast, communication involves a signaller-actor who capitalises on the senses and muscles of a perceiver-other. Only if the latter has evolved to respond to the actor's behaviour can one conclude that true communication has occurred. As Scarantino argues, however, even in cases of clearly coercive behaviour, possible perceiver specialisation cannot be ruled out. In fact, one can argue that such cases are particularly likely to create selection pressures shaping reactor responses over evolutionary time. We must also point out that while it is difficult to rule out possible reactor specialisation in coercion, ruling it in even in archetypal cases of communication can be still more challenging. In predator-specific alarm signalling in vervet monkeys, for example, adaptive

specialisation is clearly evident on the production side. Vervet infants produce recognisable, predator-appropriate alarm calls without first needing to experience how others use them or to practise making these sounds. In contrast, there is no evidence of specialisation in responding to the calls. The same infants that competently produce the vocalisations initially show no sign of knowing how to respond when others give them. Responding is acquired over the first year of life through evidently standard, generalised learning mechanisms. In other words, there is no indication of perceiver specialisation even in this quintessential instance of animal signalling.

Michael Owren and Drew Rendall

The distinction between the ‘code model’ and the ‘ostensive-inferential model’ of communication depends primarily on whether a signal uniquely specifies the signaller’s meaning or just provides evidence for it: in other words, whether the correlation between signal and meaning is 1.0 or less than 1.0 (but not equal to 0). In both models the meaning of a signal is something (perhaps a state of mind) other than the correlation. This approach is explicit in those simulations of communication that score a successful interaction when the receiver interprets a signal in the same way the signaller does. The authors’ new model of communication makes an important improvement by incorporating ‘functional effects’ (the consequences of producing or responding to a signal). It is then easy to show that communication must have benefits for both signallers and receivers. It is important to emphasise, however, that signallers and receivers must receive benefits only on average. In this chapter, the ‘on average’ is missing from the accounts of ‘functionality’.

R. Haven Wiley

Response

I thank the commentators for their thoughtful and engaged responses to the chapter I co-authored with Simon Kirby. I have divided my responses into three main areas: (i) the difference between the code and ostensive-inferential models of communication; (ii) the role of information in communication; and (iii) various issues around the functionality of signals and responses.

First, I wish to clarify the difference between the code and ostensive-inferential models of communication. **Wiley** interprets the distinction between the two as whether or not a signal uniquely specifies the correct meaning. This is not quite right. In some computational models agents have different meaning-form

mappings, and their responses are determined probabilistically (e.g. Smith, 2005). In these models signals do not uniquely specify meaning, but these are still code models – because the basic paradigm remains one that involves ‘looking up’ signal–meaning mappings, both in production and reception. The ostensive-inferential model, in contrast, involves the expression and recognition of intentions (Sperber & Wilson, 1986). It is this difference in the way that communication is achieved that distinguishes the two models. One view that we wished to express in our chapter was that a potentially profitable avenue for future research is the development of agent-based or mathematical models of the evolution of language that are ostensive and inferential in this way.

Second, I should respond to the comments of both **Horn and McGregor** (H&M) and **Owren and Rendall** (O&R) on information. H&M appear to suggest, with a parenthetical aside, that we think that use of the term *information* is metaphorical, and so I should clarify that this is not the case. What is metaphorical is the code model of how communication works; this is not the same thing as information. Otherwise, H&M, and also O&R, agree with us that although information transfer is, on its own, an insufficient characterisation of communication, there is information in whatever correlations exist between organismic behaviour and features of the world. For H&M, this is a reason to use information as shorthand for the different ways in which external influences can affect organisms. In contrast, for O&R it is a reason to be very careful about how we use the term information. Both are correct: if we simply want to study how the inputs received by one organism affect its behaviour, talk of information is good shorthand for both signals and other sources – but at the same time, if we are focused on communication, we should not, as our chapter emphasised, equate communication with the use of information to inform behaviour.

Finally, the commentaries raise a variety of issues around the functionality of signals (and responses). The first is the need for the clause ‘on average’ in our definition of communication. Following Maynard Smith and Harper (2003), we defined communication in functional terms: as any pair of behaviours (or structures) that have symbiotic functionality. This implies that signals should on average be beneficial for both parties. Both Wiley and H&M point out that we neglected to mention this, and they are correct: ‘on average’ is a necessary clause in nearly all population-level analysis of social behaviour (Davies *et al.*, 2012). Our definition of communication is no exception.

As Wiley comments, our definition makes it explicit that communication must (on average) be beneficial to *both* parties. O&R, however, resist this conclusion, and argue that communication can be (but need not necessarily be) maladaptive for the receiver. As I argued in my commentary on their chapter, I do not see how this can be the case. Communication is a symbiotic interaction

between two organisms, and if it were not beneficial for both parties then it would collapse (Scott-Phillips *et al.*, 2012). In the specific case of receivers, this means that if responses were maladaptive (on average) then they would be selected against, and the interaction would no longer be communicative.

R&O argue against this conclusion by pointing to some uncontroversial instances of communication in which there is no receiver specialisation (an argument that is reflected in the title of their commentary). They illustrate this with the example of vervet calls, the response to which appears to be acquired through general learning mechanisms. I do not see the relevance of this. Our definition of communication is based upon functionality, not on the specifics of any mechanism, specialised or otherwise. The mechanisms involved in responses produce adaptive outcomes (hiding from predators), and it is at least in part because of this that they are successfully passed on from one generation to the next. This makes them functional as response mechanisms, and that is both necessary and sufficient for our definition (see Millikan, 1987, for extensive discussion of what it means for a trait to have a function). If instead the consequences of the interaction are neutral for the 'receiver', or at least insufficiently strong to undergo selection, then that would be a case of coercion.

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