

REVIEW

Defining biological communication

T. C. SCOTT-PHILLIPS

*Language Evolution and Computation Research Unit, University of Edinburgh, Edinburgh, UK**Keywords:*

animal signals;
 coercion;
 communication;
 cue;
 information;
 response;
 signal.

Abstract

Communication is ubiquitous in biology, and agreement on terms essential for scientific progress. Yet there is no agreed definition of biological communication. Definitions couched in terms of adaptation are often used, but there is significant variability in exactly which criteria are invoked. An alternative is to define communication in terms of information transfer. This article reviews the merits of these approaches, and argues that the former is to be preferred, so long as we demand that *both* the signal *and* the response be adaptive, rather than just one or the other, as is common. Specific concerns with the definition are addressed, and it is then explained why an account of communication predicated on information transfer is necessarily derivative upon such an approach. Other alternatives and some variants of the adaptationist definition are also briefly discussed.

Introduction

In their book *Animal Signals* John Maynard Smith and David Harper offered the following definition of a signal: 'any act or structure which alters the behaviour of other organisms, which evolved because of that effect, and which is effective because the receiver's response has also evolved' (Maynard Smith & Harper, 2003, p. 3). This is a definition predicated on adaptation. Interestingly, it makes no mention of information or similar concepts (Stegmann, 2005), in contrast to many other approaches: 'the concepts of *information* and *signal* form integral components of most definitions of communication... [and] we tend to think of biological signals as conveying or carrying information' (Hauser, 1996, p. 8; italics in original). These two approaches are quite different, yet a precise and agreed upon definition of communication is surely necessary. For example, the predictions made by biologists about the behaviour of organisms will depend in part on whether or not they think communication occurs (Diggle *et al.*, 2007a,b). Indeed, consensus on the meaning of terms is in general essential for scientific progress (Brown, 1983; West *et al.*, 2007). Yet there is so

little consensus on what form a definition of communication should take, that several authors (e.g. Slater, 1983; Grafen, 1990; McGregor, 2005) are pessimistic that any single definition would suffice. On the other hand, others refuse to accept that such a situation is inevitable: 'There must be something wrong [with the present ambiguity]. There must be a way of defining "communication" ' (Dawkins, 1995, p. 75).

This article shares that view, and suggests that the 'full' version of the adaptationist definition, as typified by Maynard Smith and Harper, is an appropriate way in which to define communication. In contrast, the informational view is argued to be conceptually unsound, and at best derivative upon the adaptationist approach. The article is organized as follows. The next section discusses the internal logic of the adaptationist definition of signal, and explains why it is able to deal with the three-way distinction between signals, cues and coercion in a straightforward way. Three specific concerns with the adaptationist approach are then identified: first, that the definition appears not to allow for the possibility of an *unreceived* signal; second, that a definition couched in terms of effects rather than information will be too liberal (West *et al.*, 2007; following Grafen, 1990); and third, that the third clause in the definition brings with it some ambiguity in conflict scenarios (Stegmann, 2005). All of these concerns are given responses that leave the adaptationist account unaffected. The informational view

Correspondence: T. C. Scott-Phillips, Language Evolution and Computation Research Unit, University of Edinburgh, 40 George Square, Edinburgh EH8 9LL, UK.
 Tel.: +44 (0)131 650 3956; fax: +44 (0)131 650 6883;
 e-mail: thom@ling.ed.ac.uk

is then discussed, and it is explained why such a view is necessarily derivative upon an adaptationist account. Finally, some alternative definitions are briefly reviewed. The article concludes that signals and hence communication are best defined with reference to adaptation, and that if it is to be discussed at all information should be seen only as an emergent property of communication and certainly not as a defining quality. It pins down a precise definition of *communication* and a number of associated concepts, *coercion*, *cue*, *response* and *signal*; these are summarized below.

Coercion: Any act or structure that (i) affects the behaviour of other organisms; (ii) evolved because of those effects; but which (iii) is effective for some reason other than that the effect has evolved to be affected by the act or structure.

Communication: The completion of corresponding signals and responses.

Cue: Any act or structure that (i) affects the behaviour of other organisms; and (ii) which is effective because the effect has evolved to be affected by the act or structure; but which (iii) did not evolve because of those effects.

Information: A reduction in uncertainty.

Response: Any act or structure that (i) is the effect of some act of structure of another organism; (ii) evolved to be affected by that act or structure; and (iii) which is affected because the other act or structure (the signal) has evolved to affect this act or structure.

Signal: Any act or structure that (i) affects the behaviour of other organisms; (ii) evolved because of those effects; and (iii) which is effective because the effect (the response) has evolved to be affected by the act or structure.

The adaptationist approach

Although the Maynard Smith and Harper definition quoted above provides some of the inspiration for the present article, it is not quite precise enough for the present purposes. The following is therefore used:

A signal is any act or structure that (i) affects the behaviour of other organisms; (ii) evolved because of those effects; and (iii) which is effective because the effect (the response) has evolved to be affected by the act or structure.

The only substantial difference between this definition and Maynard Smith and Harper's wording is the explicit requirement that the response not simply be adapted but be adapted to fulfil its half of the communicative dynamic. That much is implied by Maynard Smith and Harper, but it is best that such criteria be made explicit. We will see why this particular criterion is necessary when the concerns with this definition are addressed.

It is worthwhile to note that the definition is simply the logical conclusion of a number of adaptationist definitions that stretch back to many years. Such defini-

tions take as their starting point the idea that a signal must influence the behaviour of another organism. This, however, is insufficient on its own, as it does not distinguish between, say, a push and a signal that tells another organism to move. This is why several authors have added a further criterion that the behaviour be selected in order to influence the other organism (e.g. Krebs & Davies, 1993; Hasson, 1994; Shettleworth, 1998). This additional criterion introduces adaptation to the definition. However, the receiver's role in the interaction is not yet given the prominence required. Communication is 'neither the signal by itself, nor the response, it is instead *the relationship between the two*' (Wilson, 1975, p. 176, italics added). We should therefore demand that the roles of *both* the signaller *and* receiver be necessary for communication to occur (although Wilson's own definition only demanded that the signal be adaptive for either one or both participants). That is, there is no communication if either signaller or receiver is missing from the equation. The natural idea that a signal is something that is 'projected' into the world to be 'consumed' by possible receivers is apt to lead us astray, in that it renders us liable to forget or neglect the fact that for a communicative dynamic to exist in the first place there must first be *both* a signaller and, less obviously, a receiver.

This two-pronged nature of the definition of a signal is why Krebs & Dawkins (1984), in a landmark paper, were able to describe animal communication as the result of an evolutionary arms race. In an earlier piece (Dawkins & Krebs, 1978) they had focused on the signaller's behaviour and whether it is better described as information or manipulation. In the later article, they promote the receiver's role from passive receptacle to active player. Specifically, they characterize the receiver as 'mind-reading' the signaller, as a counter-balance to the signaller's 'manipulation'. Communication thus becomes the result of an arms race between these two behaviours. Although Krebs and Dawkins' conception of animal communication is often said to assume that all communication entails conflict of interest (e.g. Haven-Wiley, 1983; Slater, 1983; Grafen, 1990; Shettleworth, 1998), its underlying logic is the same as Maynard Smith and Harper's. There have been isolated examples (e.g. Lewis & Gower, 1980; Grafen, 1990; Dusenbery, 1992; Maynard Smith & Harper, 2003) of definitions that demand that the interaction be adaptive for both parties, but such a 'full' definition is yet to be commonly adopted.

In the next section I show that such a definition works, in the sense that it is able to address a number of specific concerns. Before then, it is worthwhile to note that the symmetrical format of the definition allows for a straightforward distinction between signals, cues and coercion. This can be seen in Table 1 (Diggle *et al.*, 2007a). The second clause is used to distinguish a signal from a *cue* (Hasson, 1994); an example would be, say, height: the size of a predator could be useful information

Table 1 Distinction between signals, cues and coercion.

	Signaller's behaviour evolved for purpose of affecting receiver?	Receiver's response evolved to be affected by signaller's behaviour?
Signal	Y	Y
Cue	N	Y
Coercion	Y	N

Adapted from Diggles *et al.* (2007a).

for prey (*information* is used here in a colloquial sense; it is not intended to hint at a connection with other uses of the term that shall be employed shortly; *data* could be used in its place if necessary), and may hence cause an effect in the prey, but we would not wish to say that the predator signals its height to the prey. (This would be doubly true if the predator had not even seen the prey, but had only been seen.) We may draw a similar distinction with the third clause: *coercion* refers to the scenario where the receiver is not adapted to respond to the signal. One example would be the push/tell distinction mentioned above. Another would be camouflage: camouflage affects the behaviour of the other organism – predators are less likely to eat camouflaged prey – and camouflage evolved for that reason (Hasson, 1994). However there is no evolved response (Maynard Smith & Harper, 2003). The predator is coerced not to pursue the prey. The predator may, of course, have evolved heuristics to determine the nature of, or how much time to spend on, its search for (camouflaged) prey. However, this behaviour is not a response to the camouflage – it did not evolve *to be affected* by the camouflage. On the contrary, these behaviours (presumably) evolved as counter-measures. This example serves to illustrate why we should demand that the response be not just evolved, but evolved specifically to form one half of the communicative dynamic. A similar example is reciprocity, which will be discussed shortly.

Concerns with the adaptationist approach

Concern 1: the impossibility of an unreceived signal

A first concern with such definitions is that the insistence on a dyad does not allow for the possibility of an *unreceived* signal. Although I have not found an instance of this concern in the literature, it is worthy of a brief discussion because it makes clear the distinction between signalling and communication. The concern is that if signals have, by definition, a corresponding response then what are we to make of scenarios in which something we would like to call a signal is produced but where the intended receiver pays no attention or does not notice the purported signal? On the definition under consideration it would appear that we cannot call this a signal, however much it may be intuitive to do so.

However, we may say that the signal will induce the response *on average*. That is, although a signal may on occasion fail, perhaps due to noise or poor design, on average it will induce a response and will hence undergo selection. In other words, failure is unexpected but possible.

It is this potential failure that marks the distinction between *communication* and *signalling*, which are otherwise synonymous. Both refer to the production of a signal which is designed both to utilize and to be utilized by the receptive capabilities of another organism. Signalling, however, may occasionally fail, despite its design. Communication, in contrast, refers to the successful completion of a signalling act. This implies that there is no such thing as failed communication, only failed – that is, unreceived – signalling. This distinction also allows us to pin down the corresponding definition of a response: an act (or structure) that is caused by a signal and is adapted to be so. Or more precisely, a response is any act or structure that: (i) is the effect of some act or structure of another organism; (ii) evolved to be affected by that act or structure; and (iii) which is effected because the other act or structure (the signal) has evolved to affect this act or structure.

Concern 2: substantive effects are too liberal – the case of reciprocity

A second concern with the adaptationist definition of communication is that any definition based on substantive effects rather than information will be too liberal. An example of this would be reciprocity (West *et al.*, 2007; following Grafen, 1990): the exchange of otherwise altruistic behaviours (Trivers, 1971). How might this satisfy the definition? A behaviour that will form one half of a reciprocated pair affects the future behaviour of the other individual. We may also suppose that it evolved to do just that (after all, in and of itself it has negative fitness consequences, so it is unlikely to be the result of drift or other non-selective evolutionary forces). Finally it would seem, at least at first glance, that the 'response' – the reciprocation – evolved as part of the same dynamic. Yet we would not, *prima facie*, want to term reciprocal behaviours communicative. However, a more careful examination of this case shows that it does not satisfy the third condition.

This is because the selection pressure that acts on the 'response' is not – contra-intuition – to have one's behaviour altered by the 'signal', as required by the definition. Rather, it is to reverse the dynamic and alter the other player's behaviour. In other words, reciprocation is not communicative but actually consists of the iterative coercion of each other's behaviour. This argument requires some expansion. In a reciprocal relationship each behaviour carries a negative cost to the actor and a positive benefit to the receiver. The roles of actor and receiver are alternated, so that the series of payoffs

for each participant alternates between positive and negative. Now, let us examine in detail the situation after each positive payoff, where one participant has received a benefit from the action of the other, and is now due to pay a cost. What selection pressure(s) induce the individual to perform the costly action that is required to maintain the reciprocal relationship?

The answer to this question is *not* that the selection pressure is to reward the other participant's cooperation. That is a costly act, and will be selected against. Instead, natural selection must be sensitive to more than the immediate payoffs (which are negative), and somehow account for the medium- or long-term expected future benefits of the relationship (which are positive). [The obvious way in which this could be done would be if individuals are able to remember the past behaviour of others (Silk *et al.*, 2000) and/or learn from others' experiences (Enquist & Leimar, 1993).] This expectation that the act will produce future benefits for the actor is not the same selection pressure as one that rewards the other participant. On the contrary, sensitivity to expected future benefits entails that the individual induce the other participant into a further iteration of the relationship.

To be clear, there are two possible selection pressures. One is to reward the other participant. The other is to induce the other participant into a further act of altruism. The first of these cannot be stable; the second may be (subject to other criteria, specifically that the net payoff to each participant be positive). Yet the criterion that the response be evolved *to be affected by the signal* corresponds to the first of these selection pressures, and is consequently unstable. Instead, in order that the relationship be stable the 'response' must be under a pressure to induce certain behaviours in the other participant (namely a further iteration of the relationship). Therefore the costly act in each iteration of reciprocation does not satisfy the third condition of the definition of communication. Reciprocity is not communicative.

Note that this case illustrates the need for the third clause in the definition to explicitly demand that the response be adapted *to utilize the signal*, and not simply be adapted. That is, the question about whether a behaviour is a response to a signal must be answered in terms of selective forces rather than in terms of a proximate, mechanistic cause-and-effect relationship. Only if the selective forces behind the behaviour are to be affected by the purported signal can we term the interaction communicative. Instead of asking 'In what circumstances has evolution caused the response to be given?' we must ask 'Why is the response selectively advantageous?' In most cases these two questions will lead to the same answers, but there will be instances – like that of reciprocity – when they do not. As a result, without this criterion reciprocity would indeed satisfy the definition.

Note also that this analysis implies that reciprocity may be characterized as the iterative coercion of one another's

behaviour, as it satisfies the first two clauses of the definition of communication but not the third. That is, each costly act influences the behaviour of the other organism and is adapted to do so. (We may assume that it is adapted to do so, as otherwise it would have been selected against – on its own it is costly to perform.)

Concern 3: ambiguity in conflict scenarios

The final concern is that the definition's third condition, that the receiver's response should have evolved, introduces a degree of ambiguity in scenarios where the participants' interests conflict (Stegmann, 2005). This is supposedly because whether or not the receiver responds to the signal will depend on whether or not they are likely to emerge from the encounter victorious or defeated. The argument is illustrated with the example of male red deer, which roar at each other as a form of competition for females (Clutton-Brock & Albon, 1979). Those that roar less frequently and with greater formant dispersion eventually give up and leave the females to those deer that roar more frequently and with lower formant dispersion (Reby & McComb, 2003). Uncontroversially we can accept these roars as signals on the adaptationist account. But sometimes roaring (and the associated parallel walking) does not settle the contest. In this situation the two males engage in a fight, with potentially high costs: they push against each other head-on. One male will push the other back and at this point the loser retreats. It is argued that the criterion that the receiver's response has evolved renders the signalling status of examples like this ambiguous (Stegmann, 2005). On the one hand, the pushing behaviour of the eventual winner does not appear to be a signal because it does not change the behaviour of the losing deer, which continues to push as hard as it can. Any backward movement is due not to the result of a change in the loser's pushing behaviour, but instead to coercion by force. On the other hand, if the loser makes an active retreat then the pushing behaviour of the winner has made a difference to the loser's pushing behaviour, as the loser has ceased to push. Hence, whether or not the pushing behaviour satisfies the definition appears to depend upon the eventual outcome of the contest.

This reasoning is not quite right, and here is why. Both animals wish to maximize their payoff from the encounter. That payoff includes not just the benefits of access to females or territory, but also the minimization of the costs required to realize those benefits. Hence their first interaction is not to fight each other, but to display to each other, in a cost-free way, some correlate of their fighting ability. By doing so, the two protagonists may draw conclusions about who would win a fight (and hence who will get the access to the females) without having to engage in the fight itself. This is one reason why dogs display their teeth and not, say, their tails: the

former are indices of fighting ability but the latter are not. Similarly, the formant dispersion of a red deer's roar is reliably (negatively) correlated with its size (Clutton-Brock & Albon, 1979), and large deer tend to win fights against smaller deer. It is therefore in the interests of the deer with the greater formant dispersions to retreat. It is only if neither party is willing to back down that the deer begin to push each other. In effect, this scenario emerges only when both parties consider the potential payoff to outweigh the cost and uncertainty of a fight. Hence, the deer lock horns.

This decision may be reversed at any time. Specifically, if it becomes clear that the other deer is a more able fighter – as it does when one deer is pushed back by the other – then the losing deer should choose to retreat from the scene. Crucially, this decision to retreat once pushed back is *not*, against the concern in question, an evolved response to losing the fight. Rather, it is an evolved response to the new information (again, this is only a colloquial use of *information*) that the deer has obtained by engaging in the fight: that the other deer is the stronger. The distinction between this information and the defeat itself is subtle but important. The bottom line is that any animal that is adapted to its surroundings will depart any scene if the inputs to its system suggest that it should do so. The red deer's retreat is a behavioural strategy that is independent of whether or not the scenario is communicative.

Moreover, to suggest that the retreat is a response to defeat is to suppose that the defeat *preceded* the retreat. In fact, the retreat is precisely what marks the defeat as being so. As such, it is analogous to a performative speech act; that is, a speech act that is self-fulfilling like, say, 'I surrender' or 'I declare this ship...'. The production of such utterances automatically fulfils the very speech act that they constitute (Austin, 1955). Similarly, the deer's retreat *constitutes* its defeat. In sum, then, the pushing is not a signal even on Maynard Smith and Harper's full definition. Instead, it is coercive, and the concern that the third condition introduced unnecessary ambiguity is unfounded.

On the contrary, the third condition is entirely necessary. The preceding discussion shows that it allows us to exclude troubling examples like conflict scenarios, reciprocity and camouflage from our definition. Furthermore, as already noted, the third condition gives a dyadic form to the definition that mirrors the essential nature of evolved communicative dynamics. The adaptationist account is, then, able to resist the specific concerns that have been considered. It thus appears to be an appropriate way in which to conceptualize animal communication. Yet several authors (e.g. Smith, 1977; Hauser, 1996; McGregor, 2005) have noted that many definitions of communication invoke the transfer of information instead. The next section examines the merit of such an idea.

Information and other alternatives to the adaptationist approach

The informational approach to communication

Here are three examples of the informational definition of communication: 'behavior that enables the sharing of information between interacting individuals' (Smith, 1977, p. 2); 'the transfer of information via signals sent in a channel between a sender and a receiver' (Hailman, 1977, p. 52); and 'the behaviors by which one member of a species conveys information to another member of the species' (Kimura, 1993, p. 3). There is, for some, an intuitive sense in which any adaptationist account of signalling and communication is 'incomplete' (Stegmann, 2005, p. 1016) as the content of the signal appears to be 'missing' (p. 1015) and the definition 'has nothing explicit to say about the [signal]'s information itself' (p. 1017). Hence if our intuitions are any guide then perhaps it is desirable to invoke information, even if we do not need to. Indeed, information does appear to offer something that the adaptationist definition does not: specification of a given signal's content at a very fine-grained level (for a wide range of examples and extensive discussion see Bradbury & Vehrencamp, 1998; chapter 13). Yet the logical conclusion of adaptationist accounts of communication is to eschew the notion of information altogether and instead focus only on behaviours and adaptation (Dawkins & Krebs, 1978). This does not imply that information is not part of communication; only that it need not (and, as we shall see, should not) be definitional. This section explains why that is so.

The argument, in short, is that in order to specify exactly what information is transferred we first have to specify the signal's function, which brings us immediately back to the adaptationist definition. To begin, we must first define information. Appeals to intuition are insufficient here if our goal is to derive a precise definition of communication, so we cannot simply invoke some 'everyday' sense. More formally, information is considered to be equivalent to a reduction in uncertainty (Shannon & Weaver, 1949). But uncertainty of what? Such a definition is incomplete without a statement about what is relevant. A simple thought experiment illustrates the problem. What uncertainty is reduced if I receive an email from a friend with instructions about where to meet for dinner this evening? Most obviously, there is a reduction in the uncertainty of where I should expect to find my friend this evening, but there is also a reduction in uncertainty about many other things: the correct functioning of my computer, the correct functioning of my email program, the correct functioning of the satellites that carried the message in its digital form, the continued non-existence of a meteor in the location previously occupied by the satellite that carried the message, and so on.

[This is analogous to a famous problem in the philosophy of language, that of referential indeterminacy (Quine, 1960). The thought experiment runs as follows: an anthropologist sees a member of a tribe, whose language he does not know, shout the word 'gavagai' just as a rabbit runs past. What does 'gavagai' mean? Although we would intuitively say 'rabbit', we cannot know this deductively. We instead have to make an inductive leap, and hence our conclusion about the meaning of gavagai is not logically determined. It could, after all, mean 'fluffy thing', 'dinner', 'undetached rabbit parts' or any one of an actually infinite number of possibilities.]

Hence although a signal most certainly conveys information, exactly what information it conveys is determined at least in part by the receiver: if I wish to know about the correct functioning of my email program (it may have recently played up on me, say) then my friend's email is informative in that regard; if, on the other hand, I have no concerns about my email program then the email is not informative (in that regard). This is all, of course, in addition to the information about dinner that forms the body of the email, which we assume to be relevant. But why do we assume that the body of the email is relevant? Only because it would be unusual indeed for my friend to email me about where to meet if we had no previous plans to meet at all, or if my friend knew I was busy elsewhere, or if, even, my friend was busy and could not meet me. In short, we assume that the signal is in some way designed to achieve a particular purpose. Other aspects of the signal (like, for example, its appearance in my email program in an apparently normal manner) may carry other sorts of information; specifically, they may carry information that was not part of the signaller's design of the signal (i.e. about the normal functioning of my email program). These sorts of inferences are the human equivalent of a cue.

Therefore in order to argue that communication entails the provision of information we must also specify what is relevant about the signal, otherwise we are left with a definition so broad that it includes cues: traits or behaviours that are informative but are not designed to be so. How do we define what it means to be relevant? Relevant signals are those that are of use to the receiver; irrelevant signals those that are not. And of course, if the receiver has nothing to gain from the signal then we should expect the receiver to adapt to ignore the signalling behaviour. Correspondingly, the signaller will cease to perform the behaviour. Hence relevant signals are those that are adaptive for the signaller to perform *and* for the receiver to respond to. If the communication is not in the interests of one or the other organism then any signalling or responding behaviour will be maladaptive: even if there are no direct costs to being ignored (as a signaller) or drawing false conclusions (as a receiver) then the behaviour will

still be maladaptive rather than neutral because of opportunity costs and wasted energy (Maynard Smith & Harper, 1995).

We have now arrived back at the non-informational, adaptationist definition of communication: the signal must be designed to have an effect on the receiver, and the receiver's response should also be designed to utilize the signal appropriately. In other words, when we flesh out a definition of communication based upon the transfer of information then we see that it collapses to the non-informational adaptationist definitions that we already know are sufficient to define communication. Or to put it another way, the adaptationist definition necessarily incorporates the informational definition. If we insist that information is transferred in communication – and we need not, as the adaptationist account makes clear – then the best we can say is that it is an emergent feature of communication, and 'not an abstraction that can be discussed in the absence of some specific context' (Hauser, 1996, p. 6). Consequently an informational account that does not discuss adaptation necessarily brings with it a degree of ambiguity, as we cannot even specify what the informational content of a signal is *until* we have specified what the signal is (adapted) *for*.

As an example, consider fluctuating asymmetry (FA), the deviations from perfect symmetry exhibited by almost symmetrical structures. It has been suggested that FA is a reliable proxy measure of homeostasis (Mather, 1953), and hence that organisms that exhibit low FA should be more attractive than those with high FA scores (Møller, 1993). Is symmetry a signal? In the absence of any behaviour that brings attention to symmetry, the intuitive answer must be no. But on an information-based view the answer will often be yes: FA carries information, that information is of value to the receiver (the potential mate), and conveying that information would be beneficial for at least some senders; specifically those with low FA scores. In contrast, FA does not qualify as a signal on an adaptationist definition unless there is a specific display that brings attention to it. (In this case we may even wish to argue that the display is the signal, rather than the FA itself, though whichever we prefer the argument is not changed.) In the absence of a display, FA should instead be seen as a cue (Maynard Smith & Harper, 2003). This example illustrates the general problem with information-only definitions: they do not specify how or why a signal is relevant, and hence they have no consistent means by which to distinguish between signals, cues and coercion.

Other alternatives to the adaptationist account

One historically popular view is that signals should be conspicuous, exaggerated or stylized. This idea arises from early ethological work on how signals first emerge

(Tinbergen, 1952; Huxley, 1966), which emphasized the fact that signals are likely to be derived from other behaviours and that once they have obtained their new function are likely to increase its salience in order to have the communicative effect desired. [The roots of this idea can be found in Darwin's (1889) *Principle of Antithesis* and are also observable in the landmark Krebs & Dawkins (1984) paper published nearly 100 years later.] However, there are plenty of subtle examples, observable only with great care or detailed video analysis, that will fall foul of this criterion. Indeed, economy of effort is often noted to be a common feature of animal signals, an observation that comes into direct conflict with the idea that signals will evolve to be highly salient (Dawkins, 1995). Relative salience is therefore an inappropriate feature with which to define signals and hence communication. Intention is another suggestion occasionally put forward as diagnostic of signalling (Batteau, 1968) but is undesirable for the simple reason that we have no reliable way in which to measure an organism's intentions. Moreover, there must be considerable doubt on whether it is even coherent to talk about the intentions of non-human species.

Other authors have suggested refinements to the adaptationist approach, despite its internal logic. Such proposals are likely to lead to a degree of confusion. Indeed, the stated aim of Maynard Smith & Harper (2003, p. 1) book was 'not to report any new facts [but rather]... to bring order out of chaos', and their discussion of the definition of an animal signal suggests that they see these proposed alternatives as a route to 'semantic confusion' (p. 6). They criticize two specific suggestions. The first is that the notion of a cue be limited to behavioural traits, a move which would allow for a distinction between cues and *signs* (Galef & Giraldeau, 2001). While there are interesting differences between physical and behavioural traits, a term is nevertheless necessary for those features that affect behaviour but are not functionally designed for this purpose. That role is presently performed by *cue*, and is widely understood as such. Moreover, this distinction is, as we have seen, utterly crucial to a rigorous definition of communication; without it we fail to represent the nature of communicative dynamics and are thus left, inevitably, with ambiguous examples like FA. A distinction between the physical and the behavioural would be of value, but redefinition of an established term like *cue* seems the wrong way in which to achieve this, particularly in a field that already has a large degree of semantic inconsistency (Maynard Smith & Harper, 2003).

The same problem bedevils the suggestion that the key distinction between a signal and a cue is not whether or not it has evolved for the given effect in question but is instead the combination of two other features: first, that cues are always 'on' while signals are switched between 'off' and 'on'; and second, that once a cue has been produced it costs nothing more to express it while the

same is not true of signals (Hauser, 1996). This plays to our intuitive idea that signals are projected into the world in some way, rather than being consistently observable features. Yet it is unsatisfactory not only because of the semantic confusion that it is likely to induce but also because there are several examples that do not fit at all easily into this new framework. For example, under this definition fixed badges of status are cues while coverable badges are signals. Yet some supposedly fixed badges can be more or less prominently displayed, according to context (Maynard Smith & Harper, 2003). Another example would be aposematic colouration. In some species, for example monarch butterflies, this is permanently 'on', while in others, for example octopuses, it is switched between 'off' and 'on'. Yet we would surely wish to use the same term for both examples. Neither is there an escape route offered by insistence that the overt display of such traits be considered the signal, for no such display takes place in the case of monarch butterflies. In sum, the distinction should be recognized but it is not definitional.

Indeed, similar criticisms will apply to most and perhaps all refinements of the adaptationist approach. This is because that approach contains within it the logical form of the communicative act, and hence any refinements will necessarily be deviations from that form. Once that occurs, ambiguous examples are likely to arise.

Conclusion

This article has sought to explain why the adaptationist approach to signals and communication works, to address some concerns that have been expressed about it, and to explain why an account based on the transfer of information is insufficient on its own. This matters because communication has previously been defined in a wide variety of ways, both within evolutionary biology and elsewhere (see Hauser, 1996 for a range of examples). Yet it is an important concept that demands an agreed upon definition.

However, it is a particularly slippery concept to define. This is in large part because of its inherent interactivity. It is for this reason that the ultimate selective pressures behind a trait must be invoked to define communication properly: without them we would not be able to distinguish cues and coercion from signals, nor exclude phenomena like reciprocity from our definition. More isolated traits are more easily defined: a heart is a blood-pumping device, for example. There is adaptation in such a definition – it goes unsaid that the heart is not a device that, on average, pumps blood in some maladaptive way – but it is implicit, and that is enough. The need to invoke selection pressures in order to provide a coherent definition marks interactive phenomena like signals and communication as being somewhat different to other, more independent traits.

Although the identified criteria have stood up to detailed analysis, it should be noted that there remains some degree of ambiguity in one specific aspect: the transition from non-communicative to communicative behaviour. Most accounts of how this occurs (Tinbergen, 1952; Huxley, 1966; Maynard Smith, 1997; Tomasello *et al.*, 1997) emphasize that communicative behaviours do not simply come into being fully formed and functional but rather tend to *emerge* from non-communicative behaviours. There will, therefore, be instances where behaviours are in the process of becoming communicative but do not yet satisfy the definition of communication. Although this fact does introduce some shades of grey at the edges of the definition, these are not the same shades that cloud the information-based definition. The transition to a communicative state only introduces ambiguity in cases where we should expect and perhaps even demand it: those where *prima facie* judgement would also be equivocal. In contrast, an information-based account is flawed in its very nature. It is adaptation that should be used to define signals, communication and associated concepts.

Acknowledgments

I wish to thank Denis Walsh, Stu West, Mike Wheeler, Jim Hurford, Simon Kirby, Tamsin Saxton and one anonymous reviewer for valuable comments on earlier drafts of this paper. This work is funded by a grant from the Arts and Humanities Research Council.

References

- Austin, J.L. 1955. *How to do Things with Words*. Oxford University Press, Oxford.
- Batteau, D.W. 1968. The world as a source; the world as a sink. In: *The Neuropsychology of Spatially Oriented Behavior* (S. J. Fre, ed), pp. 197–203. Dorsey Press, Homewood, IL.
- Bradbury, J.W. & Vehrencamp, S.L. 1998. *Principles of Animal Communication*. Sinauer Associates, Inc., Sunderland, MA.
- Brown, J.L. 1983. Cooperation – a biologist's dilemma. *Adv. Study Behav.* **13**: 1–37.
- Clutton-Brock, T.H. & Albon, S.D. 1979. The roaring red deer and the evolution of honest advertising. *Behaviour* **69**: 145–170.
- Darwin, C. 1889. *The Expression of the Emotions in Man and Animals*. John Murray, London.
- Dawkins, M.S. 1995. *Unravelling Animal Behaviour*. Longman, Harlow.
- Dawkins, R. & Krebs, J.R. 1978. Animal signals: information or manipulation. In: *Behavioural Ecology* (J. R. Krebs & N. B. Davies, eds), pp. 282–309. Blackwell, Oxford.
- Diggle, S.P., Gardner, A., West, S.A. & Griffin, A.S. 2007a. Evolutionary theory of bacterial quorum sensing: when is a signal not a signal? *Phil. Trans. R. Soc. B* **362**: 1241–1249.
- Diggle, S.P., Griffin, A.S., Campbell, G.S. & West, S.A. 2007b. Cooperation and conflict in quorum sensing bacterial populations. *Nature* **450**: 411–414.
- Dusenbery, D.B. 1992. *Sensory Ecology: How Organisms Acquire and Respond to Information*. W. H. Freeman, New York.
- Enquist, M. & Leimar, O. 1993. The evolution of cooperation in mobile organisms. *Anim. Behav.* **45**: 747–757.
- Galef, B.G. & Giraldeau, L.-A. 2001. Social influence on foraging in vertebrates: causal mechanisms and adaptive functions. *Anim. Behav.* **61**: 3–15.
- Grafen, A. 1990. Biological signals as handicaps. *J. Theor. Biol.* **144**: 517–546.
- Hailman, J.P. 1977. *Optical Signals: Animal Communication and Light*. Indiana University Press, Bloomington, IN.
- Hasson, O. 1994. Cheating signals. *J. Theor. Biol.* **167**: 223–238.
- Hauser, M.D. 1996. *The Evolution of Communication*. MIT Press, Cambridge, MA.
- Haven-Wiley, R. 1983. The evolution of communication: information and manipulation. In: *Animal Behaviour 2: Communication* (T. R. Halliday & P. J. B. Slater, eds), pp. 156–189. Blackwell, Oxford.
- Huxley, J. 1966. Ritualisation of behaviour in animals and men. *Phil. Trans. R. Soc. Lond. B* **251**: 249–271.
- Kimura, D. 1993. *Neuromotor Mechanisms in Human Communication*. Oxford University Press, Oxford.
- Krebs, J.R. & Davies, N.B. 1993. *An Introduction to Behavioural Ecology*. Blackwell, Oxford.
- Krebs, J.R. & Dawkins, R. 1984. Animal signals: mind-reading and manipulation. In: *Behavioural Ecology: An Evolutionary Approach* (J. R. Krebs & N. B. Davies, eds), pp. 380–402. Blackwell, Oxford.
- Lewis, D.B. & Gower, D.M. 1980. *The Biology of Communication*. Blackie, London.
- Mather, K. 1953. Genetic control of stability in development. *Heredity* **7**: 297–336.
- Maynard Smith, J. 1997. *The Theory of Evolution*, 3rd edn. Cambridge University Press, Cambridge.
- Maynard Smith, J. & Harper, D.G.C. 1995. Animal signals: models and terminology. *J. Theor. Biol.* **177**: 305–311.
- Maynard Smith, J. & Harper, D.G.C. 2003. *Animal Signals*. Oxford University Press, Oxford.
- McGregor, P.K. 2005. Communication. In: *The Behavior of Animals: Mechanisms, Function and Evolution* (J. J. Bolhuis & L.-A. Giraldeau, eds), pp. 226–250. Blackwell, Oxford.
- Møller, A.P. 1993. Patterns of fluctuating asymmetry in sexual ornaments predict female choice. *J. Evol. Biol.* **6**: 481–491.
- Quine, W.V.O. 1960. *Word and Object*. MIT Press, Cambridge, MA.
- Reby, D. & McComb, K. 2003. Anatomical constraints generate honesty: acoustic cues to age and weight in the roars of red deer stags. *Anim. Behav.* **65**: 317–329.
- Shannon, C.E. & Weaver, W. 1949. *The Mathematical Theory of Information*. University of Illinois Press, Urbana, IL.
- Shettleworth, S.J. 1998. *Cognition, Evolution, and Behavior*. Oxford University Press, Oxford.
- Silk, J.B., Kaldor, E. & Boyd, R. 2000. Cheap talk when interests conflict. *Anim. Behav.* **59**: 423–432.
- Slater, P.J.B. 1983. The study of communication. In: *Animal Behaviour 2: Communication* (T. R. Halliday & P. J. B. Slater, eds), pp. 9–42. Blackwell, Oxford.
- Smith, W.J. 1977. *The Behavior of Communicating*. Harvard University Press, Cambridge, MA.
- Stegmann, U.E. 2005. John Maynard Smith's notion of animal signals. *Biol. Phil.* **20**: 1011–1025.

- Tinbergen, N. 1952. "Derived" activities; their causation, biological significance, origin, and emancipation during evolution. *Q. Rev. Biol.* **27**: 1–32.
- Tomasello, M., Call, J. & Gluckman, A. 1997. The comprehension of novel communicative signs by apes and human children. *Child Dev.* **68**: 1067–1081.
- Trivers, R.L. 1971. The evolution of reciprocal altruism. *Q. Rev. Biol.* **46**: 35–57.
- West, S.A., Griffin, A.S. & Gardner, A. 2007. Social semantics: altruism, cooperation, mutualism and strong reciprocity. *J. Evol. Biol.* **20**: 415–432.
- Wilson, E.O. 1975. *Sociobiology: The New Synthesis*. Harvard University Press, Cambridge, MA.

Received 11 October 2007; revised 7 December 2007; accepted 12 December 2007