

REVIEW

Putting information back into biological communicationP. CARAZO¹ & E. FONT¹*Instituto Cavanilles de Biodiversidad y Biología Evolutiva, Universidad de Valencia, Valencia, Spain**Keywords:*

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 sensory exploitation.

Abstract

At the heart of many debates on communication is the concept of information. There is an intuitive sense in which communication implies the transfer of some kind of information, probably the reason why information is an essential ingredient in most definitions of communication. However, information has also been an endless source of misunderstandings, and recent accounts have proposed that information should be dropped from a formal definition of communication. In this article, we re-evaluate the merits and the internal logic of information-based vs. information-free approaches and conclude that information-free approaches are conceptually incomplete and operationally hindered. Instead, we propose a functional notion of information that follows logically from previous adaptationist accounts. The ensuing definition of communication provides a wider, more inclusive theoretical scope that reflects more accurately the evolutionary scenario shaping animal signals. Additionally, it is a definition better equipped to deal with the extraordinary diversity of animal signals, facilitates the distinction of honest and deceptive signals at a proximate level and accommodates a number of conceptual and practical issues (e.g. redundancy, alerting components) that are lost when we fail to acknowledge the informative content of animal signals.

Introduction

Although animal communication is arguably one of the most studied topics in the behavioural sciences, the search for its formal definition has been anything but a downhill journey. It is difficult to find a clearer example of definitions getting in the way rather than facilitating the advance of a field (e.g. Dawkins, 1995; Maynard Smith & Harper, 2003; Scott-Phillips, 2008). This notorious lack of consensus has led some authors so far as to doubt whether a definition of communication may be possible at all (e.g. Slater, 1983; Grafen, 1990; McGregor, 2005). The concept of information is at the heart of much of this controversy. Do animal signals convey information, and, if so, what type of information? Some have argued that information is a conceptual tool borrowed

from our own language, and therefore irrelevant to the analysis of non-human communication (Rendall *et al.*, 2009). However, animals often react to vocalizations and other signals in ways that strongly suggest they have acquired specific information (e.g. referential signals; Evans, 1997). In fact, most available definitions make information an integral component of communication and explicitly or implicitly acknowledge that communication implies the transfer of some kind of information (e.g. Burghardt, 1970; Otte, 1974; Hailman, 1977; Smith, 1977; Green & Marler, 1979; Halliday, 1983; Grafen, 1990; Harper, 1991; Hasson, 1994; Hauser, 1996; Johnstone, 1997; Bradbury & Vehrencamp, 1998; Greenfield, 2002). Why, then, has information proven so controversial a notion that it has led some authors to claim it should be abandoned altogether?

An attempt to grasp the nettle of the difficulty in defining communication may aid our understanding of the processes involved. Perhaps the major problem faced by information-based definitions of communication lies in specifying, of all the information potentially available to the receptor in a communicative interaction, the subset that should be considered relevant to the

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communicative context (Dall *et al.*, 2005; Scott-Phillips, 2008; Rendall *et al.*, 2009). Most discussions of the role of information in communication acknowledge that information can be used in two different senses that have and still are frequently conflated (for an excellent review, see Dawkins, 1995). The first of these is a 'technical' sense that equates information transfer with the reduction in the uncertainty that an external observer experiences as a result of witnessing an act of communication. Uncertainty can be reduced about the subsequent behaviour of the sender (broadcast information) or the receiver (transmitted information). Although this approach may be useful in some contexts (Dall *et al.*, 2005), it fails to specify the kind of uncertainty that is relevant to receivers (Dawkins, 1995; Scott-Phillips, 2008). Any given signal may reduce our uncertainty about a huge number of aspects, most of which are probably irrelevant to the communicative context (e.g. the fact that the sender is alive). Thus, the technical notion of information has proven to be excessively inclusive. This and other shortcomings prompted the adoption of a different view of information, one more akin to the colloquial sense of information. 'Semantic' information focuses on the attributes of the sender or its environment that the receiver gains knowledge of (learns about) as a result of the communicative act (Halliday, 1983; Dawkins, 1995). The semantic information presumably contained in animal signals may be about the identity, intentions or quality of the sender or about some aspect of the environment. Although considerably more useful, semantic information suffers from the same essential problem as technical information: it does not provide a way to limit precisely which information is actually being transferred to receivers (Stegmann, 2005). For example, defining communication in terms of semantic information would include 'cues' (such as the noise emitted by an owl's prey in the dark; Hasson, 1994) which most researchers agree should not be considered communicative signals (Slater, 1983; Bradbury & Vehrencamp, 1998; Maynard Smith & Harper, 2003). There have been several attempts to free the concept of some of its ambiguity, for example by introducing the notion of 'intentionality' on the sender's part, or by requiring that the communicative act must be beneficial for both sender and receiver (e.g. Halliday, 1983; Bradbury & Vehrencamp, 1998; Stegmann, 2005). However, an essential ambiguity still remains in specifying, of the whole range of semantic information potentially transmitted, the subset that receivers are actually 'responding' to.

These difficulties prompted the suggestion that information should be withheld from a theoretical framework of communication (Scott-Phillips, 2008), and recent attempts to define communication have avoided its formal use. For example, Maynard Smith & Harper (2003) recently formalized the adaptationist view of communication through 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' (p.3)

Communication, in both this and later definitions (Barnard, 2004; Searcy & Nowicki, 2005; Scott-Phillips, 2008), is defined as the completion of signals and corresponding responses. Thus, communication only takes place through the exchange of signals, which become the keystone to defining communication. Maynard Smith & Harper's (2003) definition has been termed the 'full' adaptationist definition in that it crucially demands that the communicative act must be adaptive for both parties ('true communication'; Marler, 1977; Bradbury & Vehrencamp, 1998), acknowledging that sender and receiver's interests will often diverge. It is but the logical conclusion to a long series of past adaptationist definitions (e.g. Dawkins & Krebs, 1978; Krebs & Dawkins, 1984; Grafen, 1990; Krebs & Davies, 1993; Hasson, 1994; Bradbury & Vehrencamp, 1998; Greenfield, 2002), and it effectively distinguishes between cues and signals, because only the later have evolved because of their role in communication. In addition, this definition deliberately avoids the thorny concept of information, apparently gaining in objectivity with respect to prior information-based accounts of communication (Stegmann, 2005). Maynard-Smith & Harper's 'full' adaptationist definition was recently modified by Scott-Phillips (2008) as follows:

'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.' (p.388)

The explicit requirement (already implicit in Maynard-Smith & Harper's definition) that the response must be adapted 'to fulfil its half of the communicative dynamic' is added to distinguish real communication from other phenomena (Scott-Phillips, 2008). In addition, Scott-Phillips (2008) argues that the only objective way to identify, among the vast array of potentially informative contents of a given signal, what information is relevant to receivers is to focus exclusively on the effects a given signal has on receivers (i.e. their response). Under this view, information-based definitions are depicted as ambiguous, conceptually unsound, and at best derivative of the adaptationist view, the logical conclusion being to remove the notion of information transfer from the definition of communication (Scott-Phillips, 2008).

The baby and the information bathwater

In the face of recent analyses, we feel there is a strong case to be made in favour of information. Abandoning the idea of information just because there is no agreement on its

meaning is tantamount to throwing the baby with the bathwater. Far from a semantic quibble about what words should be included in a biological definition of communication, this is a decision with deep theoretical and practical implications. To begin with, there is an obvious sense in which information-free definitions of communication fail to capture the content of animal signals (Bradbury & Vehrencamp, 1998; Stegmann, 2005; Scott-Phillips, 2008). Despite its shortcomings, the idea that signals are 'about' something continues to have intuitive appeal and has been the basis of much productive research. Indeed, it is odd that a definition of communication does not consider information transfer when, in fact, a large portion of research into animal communication is aimed precisely at uncovering the kinds of information encoded in animal signals (e.g. Smith, 1977; Hurd & Enquist, 2001). In addition, a definition that focuses exclusively on effects and ignores the information content of signals is ill equipped to deal with some of the most interesting issues in the study of animal communication, such as deception, structural-motivational rules, redundancy, referential communication, message-meaning analyses, icons or amplifiers (discussed later).

In short, even though we agree with the essence of adaptationist views (i.e. Maynard Smith & Harper, 2003; Scott-Phillips, 2008), we disagree with the conclusion that we should focus exclusively on the effects of signals. The function (proximate or ultimate effects of a signal) and information content of a signal are not the same thing, as evidenced by the fact that the same effect (e.g. to intimidate a rival) can be achieved by signals with different informative content (e.g. size, social or resident status). Knowing that a response is adaptive is not enough, as it leaves open the question of why such a response is adaptive. In its turn, we suggest an alternative that not only falls nicely into the adaptationist view, but seems to us a logical extension of the adaptationist argument. In our opinion, Hasson (1994) and Maynard Smith & Harper (1995) already identified the answer to this riddle by stating that information should be defined in direct relation to receiver fitness (discussed later). We propose to rescue a receiver-dependent (Stegmann, 2005) 'functional' notion of information, inspired by Hasson (1994) and Maynard Smith & Harper (1995), that defines the informative content of a signal as precisely that which makes the response to a signal adaptive for receivers:

Functional information: The attribute or attributes of the sender and/or the environment that (i) correlate with one or several characteristics in the design of a given signal; and (ii) are responsible for the evolution (or maintenance) of the response to that signal (its effect).

This definition draws on previous teleosemantic and functional accounts of information (Millikan, 1989;

Hasson, 1994; Maynard Smith & Harper, 1995; Johnstone, 1997; Maynard Smith, 2000; Seyfarth & Cheney, 2003; Stegmann, 2005) and defines information in direct relation to an increase in receiver fitness, thus bringing the concept of information fully into the adaptationist realm. Restricting information to 'functional' information specifies in an objective way which information is relevant to the communicative process, casting off most of the ambiguities seemingly inherent to previous notions of information. It could be argued that, in practice, it may be difficult to pinpoint what attributes of the sender or its environment make a given signal adaptive for receivers, or what elements of the signal they correlate with. However, these are questions that not only can be answered empirically, but actually drive most current research on animal communication (Searcy & Nowicki, 2005). Additionally, by putting information under the umbrella of adaptation, we can redefine signals (and thus communication) in relation to the transfer of information without the perils involved in past information-based definitions:

Signal: Any act or structure that (i) affects the behaviour of other organisms; (ii) evolved (or is maintained) because of those effects; (iii) is effective because it transfers [functional] information to receivers.

Incorporating a functional concept of information not only provides a synthetic definition of communication that brings together adaptationist and informational approaches, also has a number of advantages that we deal with in the following sections.

Trading information for effects: on the needs for a functional concept of information

Conceptually, a definition exclusively couched on effects fails to capture the double nature inherent to any communicative context. From a sender's point of view, the key factor that drives the evolution of a signal is the effect that such a signal will have on receivers (i.e. the response); any increase in the biological fitness of a sender will be attributed to the effect or effects a given signal has on the behaviour and/or the physiology of the sender. However, from a receiver's point of view, the key factor is not the effect but the information (in a functional sense) that is being extracted; any increase in receiver fitness will be predicated on such information (e.g. Johnstone, 1997; Seyfarth & Cheney, 2003). This difference is crucial to understanding the selective pressures shaping the evolution and design of animal signals. The fact that the same functional outcome (i.e. effect) can in principle be achieved by signals with different information content is in itself proof that effects and information can be dissociated. Senders will not be selected to provide information, but to trigger an effect,

whereas receivers will only respond (and thus provide the effect that makes signalling adaptive for the sender) if they can extract enough information so as to make adaptive decisions. As noted by Slater (1983), the essence of animal communication may be the influence of senders on receivers, but such an effect is achieved by releasing information to receivers. The fitness currency of senders is different from that of receivers. In a way, communication can be seen as the trading of information for effects, as receivers need information if they are to exhibit adaptive responses.

An example may clarify the dynamics of communication and the selection pressures involved. The calls of male anurans have evolved to affect females (i.e. the calls' acoustic properties seem to tap on the auditory system of their intended receivers; Ryan & Rand, 1993; Wilczynski *et al.*, 2001), yet we do not conceive of females as passive receptors of male signals. Senders emit signals because they benefit from eliciting specific responses in receivers. In our example, calls are beneficial to males because they allow them to attract females (the effect) but, what do females have in return? Receivers are selected for their ability to exhibit 'informed' decisions about how to respond to senders. If females respond to the males' calls, it usually is because it is in their best interest to do so. For example, females may obtain functional information on the presence, location, species identity and even the size of calling males (Arak, 1983). Selection will not necessarily favour males who are better at transmitting accurate information to females (and, incidentally, to other non-intended receivers such as predators). Males will be selected to influence female behaviour by tapping into the females' pre-existing dispositions (some types of calls, for example, may be more attractive to females than others; e.g. Wilczynski *et al.*, 2001), but their attempts to manipulate females put males in a position that allows females to extract information from the communicative exchange. Revealing information about themselves is probably not part of the aims, proximately or ultimately, of calling males, but it is the price they pay for attracting females. To fulfil their half of their communicative process, females need something out of the exchange. That 'something' that makes responding to males' vocalizations adaptive for females we call 'functional information'. From an evolutionary viewpoint, senders and receivers effectively trade information for responses (Johnstone, 1997; Seyfarth & Cheney, 2003).

Dawkins & Krebs (1978) famous study has been often singled out as the starting point for the demise of information-based definitions of communication. However, Dawkins & Krebs (1978) did not actually reject the notion that signals convey information. Their main concern was the ritualization process and the way it affects signal design. An influential view among ethologists was that signal design evolves to increase the amount of information available to the receiver or to

reduce its ambiguity. Instead, Dawkins & Krebs argued that the key concept to understanding signal design is the co-evolutionary arms-race between the selfish (and often opposing) interests of senders and receivers. In essence, Dawkins & Krebs' view (1978, 1984) can be just as well portrayed as a co-evolutionary arms-race between the maximization of an effect on the part of senders, what they called 'manipulation', and the acquisition of functional information on the part of receivers, what they called 'mind-reading' (what, if not, are receivers reading at all?). In our view, a definition of communication that does not capture the fundamental difference between the selective pressures acting on senders and receivers cannot be complete. An additional drawback of information-free definitions is that they fail to acknowledge the fundamental difference between the strategic and efficacy components of animal signals, which reflect qualitatively distinct selective pressures responsible for their design (Guilford & Dawkins, 1991). In contrast, a functional definition of information can easily fit with the concept of strategic design in animal signals. In fact, strategic design can be depicted as any characteristic in the design of a given signal that is relevant to its informative content.

The problem with deceptive signals

Recent empirical evidence reveals conflicting interests between senders and receiver in practically all communicative systems (Searcy & Nowicki, 2005). This divergence of interests is what drives the emergence of deceptive signals within stable communicative contexts. The study of the evolutionary mechanisms that bring about and maintain certain levels of dishonest signals in a communicative context is one of the hottest topics in the study of animal communication (Searcy & Nowicki, 2005). One problem with information-free views of communication is that, by focusing exclusively on the effects of signals, they complicate the distinction between 'honest' and 'deceptive' signals: cases in which the response (i.e. the effect) may be the same, but in which the content of the signal is different for receivers (Hasson, 1994; Searcy & Nowicki, 2005). For example, most males of the Augrabies flat lizard (*Platysaurus broadleyi*) exhibit colouration patterns that allow sexual discrimination at a distance (Whiting & Bateman, 1999). However, some males (i.e. she-males) delay the onset of adult male colouration and mimic the visual appearance of females, which allows them to deceive other males and occasionally court females in the face of residents (Whiting *et al.*, 2006, 2009). Similarly, male domestic fowl (*Gallus domesticus*) lure females by emitting food calls in the absence of food (Searcy & Nowicki, 2005). Females respond to these signals in exactly the same way they respond to reliable signals because both are physically indistinguishable, as do male Augrabies lizards when responding to she-males' visual appearance. The only

difference between reliable and unreliable instances of the same signal is the sex of the sender in the first example, or the presence of food in the second (i.e. the informative content of the signal to receivers). Introducing a functional definition of information allows us to distinguish between these two types of signals at the proximate level by depicting deception as any decoupling between the signal and its functional value to the receiver (Searcy & Nowicki, 2005):

Deceptive signal: Any act or structure that (i) affects the behaviour of other organisms; (ii) evolved because of those effects; (iii) is effective because the effect (the response) has evolved (or is maintained) to be affected by the act or structure; but (iv) does not transfer any [functional] information to the receiver.

It is worth noting that both honest and deceptive signals are instances of the same act or structure within a stable communicative context that, on average, does transfer functional information to receivers. A signal will evolve within a communicative system if it ultimately increases the biological fitness of both senders and receivers, even if the signal is dishonest at times (Searcy & Nowicki, 2005). Thus, when receivers are not able to discriminate deceptive from honest signals, from an ultimate evolutionary point of view they actually are the same signal – an idea already implicit in Maynard Smith & Harper (2003). However, at a proximate level, it can be important to distinguish between dishonest and honest signals.

When the distinction between honest and deceptive signals is dichotomic (signals either carry or do not carry information), the reliability of honest signals may vary according to the degree to which the selfish interests of senders and receivers overlap (Searcy & Nowicki, 2005). In the theoretical framework we propose, the ‘reliability’ of a signal could be depicted as the strength of the correlation between the signal (i.e. one or several of its structural characteristics) and that which makes the response adaptive for receivers. For example, if begging calls were to exist in an asexual bird species where chicks are identical genetic copies of their parents, we would expect to find that one or several characteristics of the structural design of begging calls (e.g. the frequency or the intensity of the calls) strongly correlate with the nutritional needs of a chick. In other words, the reliability of such a signal would be high. Signal reliability may decrease to the extent that senders and receivers’ interests diverge. Thus, begging calls in a sexual bird species are bound to be less reliable than those of our hypothetical asexual species, because some level of parent–offspring conflict is expected. It is worth noting that, even when interests overlap completely, a certain degree of uncertainty will always persist, so that signal reliability will never be perfect. This will be attributed to the underlying imperfections in the efficacy (not in the

strategic) design of animal signals and will depend on the intrinsic characteristics of the communicative context (Guilford & Dawkins, 1991; Wiley, 1994). Similarly, each communicative context will have a threshold below which signal reliability will be so low that it does not pay off receivers to respond, which will trigger either the evolution of higher reliability levels or the disappearance of the signal. In short, the reliability of a signal may vary continuously according to the characteristics of each communicative context, but this inherent variation does not dissolve the dichotomy between deceptive and honest instances of a given signal. At the proximate level, honest signals will always carry information, even if they do so with varying reliability. Deceptive signals will not.

It may seem that an equally logical alternative would be to base the distinction between deceptive and honest signals on the consequences of responding to either (i.e. its effects; Scott-Phillips, 2008). However, couching the definition of deceptive signals on their effects (i.e. signals with negative consequences for receivers) seems to us considerably more problematic. Take any of the classical examples of aggressive mimicry. Beetles of the genus *Photuris* mimic the light signals of females of other firefly species to attract, kill and eat their males (Lloyd, 1965). One of the possible outcomes when a *Photuris* firefly attracts a prey with its lure is that the prey escapes untouched. How would a definition based on effects deal with this fact? Most importantly, what happens if the lure normally fails (notice that many deceptive signals usually fail; Searcy & Nowicki, 2005)? Adopting a functional definition of information immediately makes it obvious that the lure is a deceptive signal because, irrespective of the outcome, it does not provide functional information to the receiver. Although the distinction is still made at the proximate level, it is based on a historical hypothesis about the context in which the signal evolved. The adoption of a functional concept of information not only facilitates this important distinction, but provides a suitable theoretical framework for the study of signal reliability.

You don't know what you got until you lose it

Many animal signals contain multiple components that may (i.e. multimodal signals) or may not (i.e. multicomponent signals) belong to different sensory modalities (Johnstone, 1996; Rowe, 1999). Redundancy occurs when some of the different components of a signal carry the same informative content. Redundancy can reduce errors in the detection and recognition of animal signals, and its study is the key to understanding some of the selective pressures shaping the design of animal signals (Johnstone, 1996). For example, redundant components

may be selected for when there are high levels of habitat noise (Wiley, 1983). Obviously, the concept of redundancy rests crucially on the concept of information, without which it is impossible to define.

The concept of information also reveals itself crucial to distinguish between alerting and subsequent components of some animal displays. Introductory or alerting components do not carry any information in themselves, but are attuned with the receiver's perceptual mechanisms to obtain its attention and enhance the subsequent transfer of information. For example, the introductory bobs of assertion head bob displays in *Anolis aeneus* do not seem to correlate with any characteristic of the environment or the sender, but are exactly the type of movements that maximally stimulate a lizard's motion sensitivity in the peripheral retinal field (Fleishman, 1992). The result of such alerting components is to trigger a 'visual grasp response' that brings the rest of the display (i.e. the informative part) onto the retina's high acuity visual field (Fleishman, 1992). Likewise, amplifiers are defined as traits that do not provide information in themselves, but rather work like 'information-enzymes' by facilitating or increasing the transfer of information (Hasson, 1989, 1990, 1991). For example, body condition (i.e. nutritional status) is an important determinant of male-male contest outcome in the jumping spider (*Plexippus paykulli*). Adult males of this species exhibit a dark central patch on the ventral surface of their abdomen. Although the size of this patch remains stable, abdomen width changes dramatically with nutritional status and abdominal patches have been shown to act as amplifiers by facilitating the assessment of abdomen width (Taylor *et al.*, 2000). It is hard to envisage how a definition of a signal that does not incorporate the concept of information may be able to formally acknowledge amplifiers and their counterparts, attenuators (Hasson, 1989, 1990, 1991).

Also resting on the concept of information, there is a conceptually important distinction to be made between 'icons' and 'symbols'. An icon is a signal whose form is related to its informative content (e.g. the bee dance), whereas the contrary is true for symbols (Maynard Smith & Harper, 1995, 2003). This distinction is far from trivial, as there are probably many ways in which evolution may have favoured a connection between signal form and function (Marler, 1967; Morton, 1977). A similar case could be made for the importance of the concept of information in defining referential signals (Evans, 1997). Again and again, information arises as a notion inextricably bound to a complete understanding and sound classification of signals.

On sensory exploitation

Another concern with information-free adaptationist definitions of communication is that they risk conflating the current and past functions of a signal (e.g.

Hinde, 1981; Cuthill, 2009). For example, the third clause in Scott-Phillips (2008) definition states that the response must have evolved to be affected by the act or structure that constitutes the signal. This statement explicitly leaves out cases that we would want to consider signals, but in which the response did not actually evolve to be affected by the corresponding act or structure even though it is adaptive because of its role in communication. This includes signals that evolved to exploit a preference already present in receivers by sensory exploitation (e.g. Ryan *et al.*, 1990; Endler & Basolo, 1998). For example, female guppies (*Poecilia reticulata*) exhibit a marked preference towards larger, more chromatic orange spots in males. Orange chroma is condition dependent, reflecting carotenoid ingestion (Kodric-Brown, 1989; Grether, 2000) and parasite load (Houde & Torio, 1992) and thus appears to be an honest indicator of male foraging ability and health. However, the females' enhanced responsiveness towards orange colouration seems not to have evolved in a communicative context, but in a foraging context as a preference towards highly nutritious, bright orange fruits (Rodd *et al.*, 2002). Normally, receiver responses do evolve in response to sensory exploitation. This is because, most of the time, sensory exploitation is initially costly for the exploited sex precisely because there is an absence of functional information (i.e. the response is not adaptive for receivers; Arnqvist, 2006). Thus, receiver responses to traits that have originated through pre-existing sensory biases are likely to undergo a subsequent co-evolutionary process to avoid exploitation by senders. This evolutionary dynamic may eventually give rise to a stable signal if equilibrium is reached between the interests of senders and receivers (e.g. Macías-García & Ramírez, 2005; Stuart-Fox, 2005). Through this co-evolutionary process, functional information is attached to the stimulus that initiated exploitation by the sender, transforming it into a signal adaptive for both parties. In these cases, the receiver's response may be said to have evolved because it has been shaped (i.e. usually through a decline in receiver response; Arnqvist, 2006) in response to the exploitative trait. However, an alternative outcome is that the evolution of a trait that exploits a pre-existing sensory bias may not feed back into any form of selection in receivers simply because receiver response is adaptive from the beginning (Arnqvist, 2006). This will be the case when the evolved trait is a quality indicator; it exploits a pre-existing sensory bias but is still an honest signal, because it carries functional information from the offset, so it pays receivers to respond even if such a response had not originally evolved to serve a communicative function. This seems to be the case with orange colouration in guppies (Rodd *et al.*, 2002). Because the development of orange colouration is necessarily costly and condition dependent (as happens with most carotenoid-based colouration; Searcy & Nowicki, 2005),

orange spots most probably carried functional information about male quality from the beginning, thus making it unnecessary for female preferences to co-evolve. In the absence of sender–receiver co-evolution, evolutionary stable signals may be established in which a receiver's response cannot be said to have evolved to be affected by the act or structure so they would not qualify as signals (Scott-Phillips, 2008).

Unraveling 'information' from 'influence' and 'representation'

As already discussed, many of those who point out shortcomings in the concept of information admit that communication implies the transfer of information in one sense or another (Dawkins & Krebs, 1978, Maynard Smith & Harper, 2003; Scott-Phillips, 2008). In contrast, some authors question whether, at least in some cases, animal signals can be said to carry any information at all. Rendall *et al.* (2009) recently argued that some signals elicit responses that are automatic, reflex-like, and depend more on design features of the receiver's sensory and nervous systems than on any transmission of information. Several studies have shown that, although receivers frequently respond to signals 'as if' they contain information, senders often seem to be unaware of the informational value of their own signals (Cheney & Seyfarth, 1990; Owren, 2000). These studies suggest that non-human communication fails to exhibit the mental state attribution abilities that are fundamental to the human language (Penn & Povinelli, 2007). Hence, Rendall *et al.* (2009) conclude that at least in some cases effects are caused by signals that probably have no information content whatsoever, an idea that harks back to the sign stimulus and releaser concepts of classical ethology (Tinbergen, 1951). Instead of focusing on a view of communication that depicts senders as informing receivers, Rendall *et al.* (2009) advocate for a shift towards interpretations based on senders influencing receivers. A wide range of animal behaviours, if not all, have evolved to exert some influence over other animals and/or the environment. Only a subset of those behaviours (i.e. signals) effectively accomplishes such an influence by means of special characteristics in their design that have specifically evolved to trigger adaptive responses in other animals (i.e. functional information). That a signal influences receivers does not negate the possibility that receivers may extract some information from it. Thus, the information vs. influence debate is a false dichotomy. Still, we feel the analysis by Rendall *et al.* (2009) deserves close consideration, especially in relation to accounts of communication that are drawn explicitly or implicitly on the human linguistic concept of information (typically non-human primate studies of referential signals). For example, couching animal communication in the language metaphor more often than not leads to restrictive views of communication that do

not take into account the efficacy design of animal signals (reviewed in Rendall *et al.*, 2009).

It is worth noting that the adoption of a functional definition of information does not entail any commitment about the degree to which senders and receivers are aware of the information (in a functional sense) being conveyed. Acknowledging that signals have certain characteristics that 'inform' about the fitness payoffs associated with displaying and responding to them is independent of the actual representations or mental constructs that go on in the minds of senders and receivers. The functional concept proposed here does not circumscribe information to something that is being conveyed by the sender in the form of a representation, even if it would certainly include animal signals that actually do so. Strictly speaking, it does not even require that something must be 'conveyed' by the sender at all. The pursuit of issues such as the meaning of animal signals for receivers, their mental state attribution abilities, or the evidence for referential communication is crucial to fully understand the communicative process (Rendall *et al.*, 2009), but has little to do with the question whether signals carry functional information. Perhaps some signals do carry referential information, whereas others simply act as releasers, but all signals carry information in a functional sense. The cognitive mechanisms underlying communication are bound to vary hugely from species to species, but the adaptationist framework reflects a common ground in the evolution of all animal signals. In our view, it is precisely because of this fact that an adaptationist approach offers the best possible framework for a definition of communication.

Concluding remarks

Historically, it has been difficult to give a rigorous and all-encompassing definition of communication. We agree with recent analyses that an adaptationist approach solves many of the problems that have encumbered previous definition of communication. However, we dissent with the suggestion that the logical conclusion of this approach is to exclude the concept of information from definitions of communication. First, because the problem with information lies not on the concept itself, but on the lack of a clear, objective, and operational definition. Second, because a definition of communication that does not incorporate information seems to us unrealistic and conceptually handicapped. We suggest that a functional definition of information (Hasson, 1994; Maynard Smith & Harper, 1995) can be adopted that follows naturally from the theoretical rationale of current adaptationist views. A functional concept of information, as presented here, avoids many of the problems that have been used in the past to justify excluding information from definitions of animal communication. In its turn, it offers a number of conceptual and practical advantages with respect to information-free approaches. We believe

that a functional information concept may finally succeed in the task of providing a synthetic definition of information (and communication) that brings together adaptationist and informational views, that is both operational and objective, and that fits nicely with the evolutionary theoretical framework of current animal communication studies.

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