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Animal communication as information-mediated influence

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2.1 Introduction

Two main approaches to the definition of animal communication or signalling are generally contrasted. One is the *information-based* approach championed by theorists who think that communication should be defined in terms of information transfer between signaller and recipient. Proponents of this approach include Otte (1974), Zahavi (1987), Bradbury and Vehrencamp (1998), Hauser (1996), Seyfarth *et al.* (1980) and others. The other is the *influence-based* approach championed by theorists who think that communication should be defined in terms of influence on a recipient by a signaller. Proponents of this approach include Dawkins and Krebs (1978), Owings and Morton (1998), Maynard-Smith and Harper (2003), Owren *et al.* (2010) and others.

In this chapter I argue that animal communication should be defined neither exclusively in terms of information nor exclusively in terms of influence. Defining communication exclusively in terms of information wrongly suggests that what drives the selection of signals is the information that signals carry, rather than the fitness benefits that signals earn for their producers. Defining communication exclusively in terms of influence, on the other hand, amounts to leaving in the background precisely what must be emphasised, namely that what distinguishes communication from other forms of influence is that signals earn benefits to their producers by carrying information to signal recipients. The take-home message of this chapter is that influence-based and information-based

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definitions of communication should not be contrasted but rather combined into a theoretically richer hybrid.

2.2 Communication as information transfer

Theorists of animal communication tend to agree on what count as paradigm cases of animal signals: alarm calls, food calls, begging calls, mating calls, threat displays, dominance displays, status badges, facial, vocal and postural expressions, and so on. What is still fiercely debated is how animal communication as a whole should be defined. According to a still dominant but increasingly besieged view, animal communication should be defined in terms of information transfer.

In a popular textbook, Bradbury and Vehrencamp (1998, p. 2) argue that "[n]early all authors agree that communication involves the provision of information by a sender to a receiver". They add that the "vehicle that provides the information is called the signal" (p. 2). Hauser (1996, p. 6) similarly states that "[t]he concepts of information and signal form integral components of most definitions of communication". But what is information?

No single answer to this question can be provided. As I have argued elsewhere (Scarantino & Piccinini, 2010; Piccinini & Scarantino, 2011), information is a mongrel concept comprising a variety of different phenomena under the same heading. This being said, one species of the genus strikes me as capturing a large portion of information talk in the animal communication literature. This is the species of what I call *predictive information*. Roughly speaking, a bearer of predictive information (henceforth, information *simpliciter*) is something that can be used by someone to predict something else.[2] Since organisms live in an uncertain world, what bearers of information generally do is to change the probabilities of various states of affairs.

Thus, a signal carries information about every state of affairs the probability (P) of which it changes. Formally, X carries information about Y if and only if $P(Y \text{ given } X) \neq P(Y)$.[3] This notion of information can be quantified by taking a

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[2] A second notion of information often conflated with predictive information is that of referential information or representation (I designated it as non-natural information in previous publications, in contrasted with natural or predictive information; cf. Scarantino & Piccinini, 2010). Roughly speaking, a bearer of referential information is something that is taken by someone to stand for something else. I will not further discuss the notion of referential information in what follows.

[3] I discuss this notion in more detail in Scarantino and Piccinini (2010). Similar theories of information are articulated, in somewhat different terms, by Millikan (2000, 2004), Shea (2007), Skyrms (2010) and several other authors.

suitable function of P(Y given X) and P(Y).[4] A common, but by no means unique, measure of the information carried by X about Y is the so-called *difference measure*: $d = P(Y \text{ given } X) - P(Y)$. The higher the difference, the more information X carries about Y.[5]

An example may help. Consider a female bird who must decide which male bird to mate with. Suppose that before receiving a mating call the prior probability that a male is healthy is P(male is healthy) = 0.5. If call M increases or decreases such probability, M carries information about health. Assume that the posterior probability is p(male is healthy given call M) = 0.9. In such case, M would significantly reduce uncertainty about the male's health, shifting it from 0.5 (equal odds that the male is healthy or unhealthy) to 0.9 (high likelihood that the male is healthy). This in turn would allow the female to reliably predict that the courting male is healthy.[6]

The ability to transfer information is considered by many animal communication theorists to be a necessary property of signals, but not a sufficient one. An additional requirement is that a signal must be *shaped by natural selection*. This

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[4] As I explain in my answers to commentators, the probabilities involved in information transmission are assigned relative to background knowledge. Such background knowledge determines which possibilities exist at the source, but it is often left implicit in ordinary information talk.

[5] A complicated question I cannot fully address in this paper is how probabilities should be interpreted in the context of informational ascriptions. The short answer is that they should be interpreted in an objectivist fashion, roughly along the lines of what Carnap (1950) labelled *inductive probability*. This is the sort of probability ascribed to a state of affairs given another state of affairs taken as evidence, and a set of further states of affairs taken as background. For informational purposes, the background is the *knowledge state* of the signal recipient, the evidence is the *signal* and the state of affairs whose probability is being investigated is *what the information is about*. Subjective probabilities and inductive probabilities are normatively related, in the sense that the inductive probability of a state of affairs given a certain evidence and background knowledge is the degree of belief that is epistemically rational to have for someone with that evidence and background knowledge.

[6] The predictive information about health clearly does not exhaust the informational content of the mating call. For example, the mating call will also raise the probability that the male is ready for sexual intercourse, that the male is not being chased by a predator, that the male is awake, that the female is at a less-than-five-mile distance from the caller, and so on. For this reason, we should think of the informational content of a signal as a *vector* which specifies how the signal changes the probabilities of various states of affairs (cf. Skyrms, 2010). Most entries of the vector will not matter to the signal recipient, either because the probabilities have not been changed to a sufficient degree to make a reliable prediction, or because the states of affairs whose probability has changed to a sufficient degree are irrelevant to the recipient's decision. Some entries, on the other hand, will matter a great deal, because they represent an ecologically significant change in the probability of a state of affairs that affects the recipient's evolutionary interests.

grounds the common distinction between *signals* and *cues*. Information bearers that carry information, but did not evolve for that reason, are considered *cues* rather than *signals* (Hasson, 1994).[7]

The following definition embodies as well as any the dominant, information-based view on animal signalling:

> [Animal signals are] behavioural, physiological, or morphological characteristics fashioned or maintained by natural selection because they convey information to other organisms (Otte, 1974, p. 385)

A key feature of this definition is that conveying information is presented as the reason why signals are fashioned or maintained by natural selection. As Zahavi (1987) makes explicit, “a signal is defined as a character which has evolved *in order* to transmit information to other individuals” (1987, p. 306; emphasis added). On this view, the evolutionary point of signalling is to transfer information.

2.3 Communication as influence

In an influential paper, Dawkins and Krebs (1978) rejected the assumption that the evolutionary point of signalling is to transfer information – an assumption they associated with the “classical ethological view” of animal communication. This assumption presupposes that signaller and recipient are engaged in a *cooperative* interaction, whereas many cases of signalling occur in *competitive* interactions. In competitive interactions, transferring information about features such as, say, one’s low reproductive quality may put the signaller at a disadvantage, so it cannot be assumed that signals evolved in order to transfer such information.

Consider an unhealthy male bird that is trying to reproduce. It is not in his interest to signal that he is unhealthy, since females tend to prefer mating with healthy males. Consequently, if the type of mating call he produces is selected for, it will not be *in order* to make information about his actual reproductive quality available, but rather because it leads females to mate with him *despite* his

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[7] For instance, the dark colour of a morsel of meat may carry information about the meat being rotten, but it did not evolve in order to carry such information, so it would qualify as a cue rather than a signal. Similarly, having a large size may carry information about fighting ability, but it would qualify as a cue rather than a signal because it presumably did not evolve in order to carry such information. On the other hand, the roar of a male whose acoustic properties were shaped by natural selection for the purpose of carrying information about having a large size would qualify as a signal.

low quality. Perhaps he can achieve this objective by reproducing the calls of healthy males and being mistaken for one of them.

The evolutionary point of sending signals, Dawkins and Krebs concluded, is not to transfer information to recipients, but to get recipients to *do things that are advantageous to the signaller*. The appropriate metaphor for signalling is therefore *manipulating* rather than *informing*.[8] This led them to offer a new, influence-based definition of communication:

> Communication is said to occur when an animal, the actor [henceforth, the signaller], does something which appears to be the result of selection to influence the sense organs of another animal, the reactor [henceforth, the recipient], so that the reactors' behaviour changes to the advantage of the actor (Dawkins and Krebs, 1978, p. 283; our additions in brackets)

This definition preserves the idea that signals are fashioned or maintained by natural selection, but it replaces the assumption that they are selected because of the information they carry with the assumption that they are selected because of the fitness benefits they earn for signallers.[9] An objection quickly comes to mind. In some cases, the signaller does not gain any benefit from signalling, as when an alarm call leads the signaller to be located and eaten by the predator. But it certainly does not follow that the alarm call is not a signal. If so, asking that "reactors' behaviour changes to the advantage of the actor" seems to be asking too much.

Dawkins and Krebs dealt with this problem by arguing that the signaller's advantage must be understood as an *average advantage* over all instances of signalling of the same type. The requirement is that producers of alarm calls benefit on average from their calls thus leading to signal selection. This is compatible with tokens of the type not leading to any advantage, or even leading to detrimental consequences. From here on, when I write that the

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[8] This shift of focus took place against the background of the so-called *selfish gene* theory of evolution (Dawkins, 1976), according to which animals are machines built by genes whose only evolutionary objective is self-preservation by whatever means necessary.

[9] Even though both information-based and influence-based accounts assume that a signal is by definition an adaptation, compelling empirical evidence about a history of selection is rarely provided. This leads the whole field of animal communication to sound remarkably Panglossian with respect to the origin of signals, with potentially negative effects on the field's ability to consider mechanisms for the emergence of signals other than adaptation (cf. Gould & Lewontin, 1978). I will disregard this limitation in what follows.

signaller *benefits* from signalling, I will mean that the signaller benefits on average.[10]

Dawkins and Krebs' critique unveiled a serious problem. The assumption that signals are selected in order to transfer information suggests that transferring information is an end in itself, whereas it is quite clearly a means to an end. What drives signal selection, just as what drives the selection of other traits, is the fitness benefit associated with signalling.[11] Furthermore, in some circumstances transferring information about one's actual features will *not* lead the recipient to do what is in the evolutionary interest of the signaller, so evolutionary pressures will be at work to *avoid* transferring such information if at all possible.

This being said, we should not conclude that information is dispensable in understanding communication. Dawkins and Krebs (1978) are largely responsible for the anti-informational turn taken by the influence approach. This is because, at least initially, they presented it as an *alternative* to the information view, suggesting that it is "reasonable to eschew the ideas of information and of meaning and to think instead of the caller as 'manipulating' the behaviour of its companions" (p. 287). The implication here is that thinking of the caller as manipulating the recipient does not require positing information (and meaning) at all.

Many proponents of the influence view have echoed this anti-informational spirit. Owings and Morton (1998) write that "[t]he information concept has [. . .] become too central, deflecting our attention from the more fundamental idea of regulation" (p. 11). This passage also suggests that focusing on information takes attention away from regulation (another label for influence), and that, when picking between the two, the focus should be on regulation.

Rendall *et al.* (2009) have been especially explicit in their opposition to the information concept, suggesting that questions such as "What information do animal signals convey?" are "ill-posed" (p. 238). They have argued that the informational approach has three fatal flaws. First, it presupposes cooperation

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[10] The commonly used expression "benefits on average" is infelicitous, because there may be cases of signalling in which the benefits are very rare, but so significant from an evolutionary point of view that signalling is still selected for. Consider a signal that leads to neither beneficial nor harmful consequences in 80% of the cases, but that leads to saving the life of the signaller in 20% of the cases. Even though 'on average' the signaller does not benefit from signalling, this signal would still be selected for. I will disregard this complication in what follows.

[11] This fact was most likely clear to proponents of the information-based view. Their mistake was not to make it explicit in their definition. This omission allowed Dawkins and Krebs (1978) to mount their case against the information-based view.

between signaller and recipient.[12] Second, it relies on a concept – information – that is systematically invoked but rarely defined, thereby creating "a conceptual vacuum at the heart of the field" (p. 240). Third, the informational approach wrongly models animal signals on linguistic signals, disregarding the important differences that exist between them.

In Scarantino (2010), I discussed the arguments of Rendall *et al.* (2009) to the effect that the information concept is poorly defined and covertly linguistic, concluding that lack of definitional clarity is not a good reason to get rid of the information concept altogether, and that suitable, non-linguistic definitions of information are both necessary and possible. In what follows, I will explain why information is crucial for understanding animal communication.

2.4 Why information is crucial for communication

Dawkins and Krebs' (1978) conclusion was that signals evolve for "effective manipulation' rather than for 'effective information transfer". This view was soon criticised for neglecting the role played by recipients in signal evolution (Hinde, 1981). If signals are selected because they efficiently manipulate recipients, recipients appear to take on the role of "automata that can be manipulated to respond in ways beneficial to the signaler" (Seyfarth *et al.*, 2010, p. 4).

But recipients are selected to behave in ways that are beneficial to themselves, not to the signaller. Seyfarth *et al.* (2010) pointed out that even signals that produce a direct influence on recipients by exploiting their pre-existing sensory and neural biases (Rendall *et al.*, 2009) – e.g. courtship calls directly producing sexual receptivity, or alarm signals directly producing preparatory flight responses – must generate benefits for their recipients in order to explain why nervous systems that are directly affected by such signals are selected for.

Furthermore, most animal signals influence the nervous system of their recipients only indirectly, by affecting the decisions they make upon receiving the signal. Upon hearing a courtship call, a sexually receptive female must decide which male to pick for reproductive purposes. Upon hearing an

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[12] According to Rendall *et al.* (2009), the assumption of cooperation is revealed not only by the fact that the evolutionary point of signalling is taken to be transferring information, but also by the fact that information is often described as being 'encoded' by signallers and 'decoded' by recipients. This "implies an initial, cooperative stage of signal evolution during which signallers and perceivers converge on a common code" (Owren *et al.*, 2010, p. 764). I share the view that the coding and encoding metaphors are inappropriate. The notion of (predictive) information I have discussed in Section 2.2 does not involve any encoding and decoding operations.

alarm call, a vervet monkey primed for escape must decide which escape behaviour to choose. It is to explain these decisions that the information construct is key.

What affects the decisions of a sexually receptive female bird or an alarmed vervet monkey is the information signals transfer about, respectively, reproductive quality and predator type. As Searcy and Nowicki (2005) have emphasised, if signals did not carry any useful information, recipients would stop responding to them, and signallers would not earn any benefits from signalling, ultimately leading to the collapse of the signalling system.

In an updated version of their paper, Krebs and Dawkins (1984) seemed receptive to this line of reasoning. They acknowledged that, as signallers have an evolutionary interest in influencing recipients to their advantage, recipients have an evolutionary interest in using signals to gain information to their advantage. As they put it, recipients are *mind-readers*, where mind-reading is a "catch-word to describe what we are doing when we use statistical laws to predict what an animal will do next" (Krebs and Dawkins, 1984, p. 386).

The caveat introduced with respect to signallers' benefits applies here as well: not every token of a signal type will lead to a response that is beneficial to the recipient. For instance, a bird may take flight upon hearing an alarm call only to realise that the call was produced deceptively by a signaller as a means to eliminating competitors for a morsel of food (Møller 1988). What must be the case is that recipients benefit on average from responding to signals, just like signallers must benefit on average from signalling.

Now, which mechanisms see to it that signals are informative? One mechanism is cooperation. Even on a selfish gene view, cooperative contexts emerge by means of kinship, reciprocity or possibly other evolutionary mechanisms (see West *et al.*, 2007). When they do, the interest of the signaller to influence and the interest of the recipient to be informed coincide. In such cases, Krebs and Dawkins (1984, pp. 391–392) remarked, signallers will show "an active 'willingness' to be mind-read", and signals will resemble "conspiratorial whispers" between willing partners.

Alas, not all contexts are cooperative. In non-cooperative contexts, signalling has to be understood as emerging from a co-evolutionary race between manipulators and mind-readers. Krebs and Dawkins (1984) suggested that, in competitive contexts, signals will be shaped by effective advertising techniques, and will consequently include "redundancy, rhythm repetition, bright packaging and supernormal stimuli" (p. 386). Several mechanisms have been proposed to explain how the informational content of signals can be preserved in non-cooperative contexts (see Maynard-Smith & Harper, 2003; Searcy & Nowicki, 2005).

I conclude that even if we accept that the evolutionary point of signalling is to influence a recipient to one's advantage, it is not a good idea to eschew information altogether. Doing so prevents us from understanding the central role information plays in competitive and cooperative signalling. But should information be part of the *definition* of animal communication?

2.5 Defining animal communication

Good definitions of scientific concepts should be extensionally adequate and fruitful. Definitions can be extensionally inadequate because they are too broad – they apply to non-instances of the concept – and/or because they are too narrow – they do not apply to instances of the concept. If we defined 'animal communication' as 'animal communication', we would have produced a counterexample-proof, extensionally adequate definition. However, we would not have produced a fruitful definition on account of its patent circularity.

Fruitful definitions should non-circularly make explicit what all and only the essential properties of a given concept are, and productively embed such a concept into a network of other scientific concepts and empirically supported generalisations. A fruitful definition of 'animal communication' should tell us what animal communication essentially is, and it should lead to scientifically interesting and empirically testable predictions and explanations about the items that satisfy the definition.

Influence theorists are right to point out that any definition of animal communication presupposing that signals are selected for in order to carry information will not be fruitful, because it contradicts, or at least fails to make explicit, a central evolutionary principle according to which traits are selected because of the benefits they confer to their owners. But they have gone too far by trying to define animal communication in an information-free fashion. Definitions of animal communication framed solely in terms of influence are both unfruitful and extensionally inadequate. They are unfruitful because they neglect to make explicit what is essential about communication, namely that it is a form of advantageous influence that relies on information transfer rather than other means. They are extensionally inadequate because they count as signals things we should not count as signals, and they do not count as signals things we should count as signals.

2.5.1 Defining communication without information

I will make my case by focusing on the most sophisticated influence-based definition of animal communication currently on offer. This is the definition formulated by Maynard-Smith and Harper (henceforth MSH; 2003).

It should be emphasised that MSH, unlike many proponents of the influence approach, are clear about the importance of information in the signalling process. They explicitly argue that "the signal must carry information . . . that is of interest to the receiver" (p. 3), devoting a large part of their book to unveiling the mechanisms underlying signal reliability.

Yet, their definition of signal is information-free:

> We define a 'signal' as 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. (MSH, 2003, p. 3)

According to this definition, a signal is an adaptation for influencing the *behaviour* of another such that the response to the signal is itself an adaptation. But what does it mean to alter the behaviour of another? At first blush, anything an animal *does* counts as behaviour, understood as a goal-oriented production of a sequence of bodily movements (or lack thereof). A predator chasing its prey engages in a behaviour driven by the goal of eating the prey. A prey animal that hides motionless behind a tree engages in a behaviour driven by the goal of avoiding being eaten by the predator.[13]

Behaviours must be contrasted with *happenings*, namely things that occur to an organism without resulting from the selection of a goal on the organism's part. Happenings can be positive, negative or neutral. Positive happenings include being groomed, being fed, being protected, etc. Negative happenings include being eaten, being hit, being pushed, etc. Neutral happenings include being looked at, being passed by, being flown over etc.

To influence the behaviour of another individual, then, is to change what such individual will do next. For example, an alarm call influences the behaviour of a recipient insofar as it leads the recipient to adopt an escape behaviour rather than, say, a grooming behaviour. MSH's proposal is that a signal is an act or structure evolved specifically for changing what another individual will do next (*specialised behaviour influencing requirement*), and such that what another individual will do next also evolved (*selected response requirement*).

From the *specialised behaviour influencing requirement* it follows that influencing the behaviour of another to the benefit of the actor does not make an act or structure a signal, unless it has features specifically adapted to have that effect on the behaviour of another. For example, suppose a predator chases a prey that

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[13] Some behaviours are goal-oriented and reflex-like, such as the recoiling behaviours produced by a suddenly looming object. Other behaviours are goal-oriented but not reflex-like, as the escape behaviours of a vervet monkey upon hearing an alarm call.

runs faster, eventually leading the slower predator to stop chasing (Hasson, 1994). Running faster than a predator, however, is not a signal the prey sends to the predator.

The reason is that, although running faster than a predator is adaptive and influences the predator's behaviour to the benefit of the prey, it did not evolve in order to influence the behaviour of the predator. As clarified by Stegmann (2005), what is selected for is outrunning the predator rather than leading him to abandon the chase (even though outrunning him does lead him to abandon the chase). The point is that the adaptiveness of outrunning a predator does not hinge on changing the predator's behaviour: it would be selected for even if the predator continued running.

The specialised behaviour influencing requirement also explains why having a large size is not a signal. Even though it is an adaptation and it influences the behaviour of others in beneficial ways (e.g. it leads them to submit without a fight), it presumably did not evolve in order to influence such behaviour, and so it would not qualify as a signal according to MSH's definition.

MSH initially thought that the specialised behaviour influencing requirement sufficed for defining animal communication.[14] In 1995, they defined a signal as any "action or structure that increases the fitness of an individual by altering the behaviour of other organisms detecting it, and that has characteristics that have evolved because they have that effect" (Maynard Smith & Harper, 1995, p. 306). They then realised that this definition does not distinguish between coercion and communication, and amended it by adding the *selected response requirement*.

2.5.2 Three counterexamples: coercion, reciprocity and deception

Coercion is widely considered not to be a form of signalling. This was clear to Dawkins and Krebs (1978, p. 604), who cited approvingly Cullen's claim that "to a man the command 'Go jump in the lake' is a signal [whereas] the push which precipitates him is not." But how is a push different from a signal? According to Dawkins and Krebs, whereas the coercer only relies on his own "physical power" to achieve advantageous influence, the signaller "can exploit the senses and muscles of the animal it is trying to control" (p. 282). Communication is then "a means by which one animal makes use of another animal's muscle power" (p. 283).

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[14] In a recent paper, Owren *et al.* (2010) have re-proposed a definition of animal communication that exclusively relies on the requirement that signals are adaptations for changing the behaviour of another. I will not discuss such definition in this paper owing to space limitations.

MSH's (2003) definition aims to exclude coercive behaviours from the domain of signals by requiring that a signal is effective in altering the behaviour of another because the recipient's response has also evolved (selected response requirement). The effectiveness of coercive behaviours, MSH thought, does not depend on the presence of an evolved response. Thus, coercive behaviours are not signals.

I agree that coercive behaviours are not signals, but I will argue that they are diagnosed as such by MSH's (2003) definition. Let us distinguish two ways in which a coercive behaviour such as pushing can influence another. On the one hand, there is the *being pushed* component of the influence, which is not a behaviour but a happening. On the other hand, there is the *response to being pushed* component of the influence, which is instead a behaviour. What an animal does as a result of being pushed (or hit, or bitten, etc.) may be to give up on a certain contested resource.

According to the *specialised behaviour influencing requirement*, signals are specialised for altering the behaviour of a recipient. So if we only focused on the first source of influence – the being pushed part – coercive behaviours would not qualify as signals not because there is no *evolved* response to them, but more simply because there is no response to them at all. Being pushed is not a behavioural response to pushing any more than dying is a behavioural response to being shot. As argued by Stegmann (2005), this would make the *selected response requirement* superfluous for explaining why pushing is not a signal. The specialised behaviour influencing requirement would suffice, because pushing would not qualify as an act that alters the behaviour of another organism (it only alters what happens to another organism).

The fact that MSH considered their 1995 definition incapable of excluding coercive behaviours suggests that their interpretation of the influence exerted by coercive behaviours included *behavioural responses* to being pushed. This broadening of the scope of the analysis is appropriate, because we are considering the proposal that signals are adaptations for influencing another, so all evolutionarily relevant aspects of the influence an act or structure has on another should be taken into account.

Our focus is now on the responses organisms display to being pushed, being hit, being bitten and so on. In order for coercive behaviours not to count as signals on MSH's definition, such responses must not have evolved. The problem is that responses to coercive behaviours are as likely to have evolved as coercive behaviours themselves. Let us consider what it would take for a receiver's response to have evolved. In some passages, MSH seemed to suggest that the response to a signal must have evolved *somehow*, but not necessarily as a response to the signal. Let us call this the *generalised response interpretation* of the selected response requirement.

This is the interpretation endorsed by Stegmann (2005, p. 1022), who argues that “Maynard Smith and Harper (2003) demand only that the reaction evolved as a response to some features, but not necessarily to the signal”. Some remarks by MSH support this interpretation. For example, MSH (2003) wrote that if a stag “roars and the other stag retreats, it is a signal, because the response depends on evolved properties of the brain and sense organs of the receiver” (p. 3). Here, the behavioural response of retreating evolved only in the sense that retreating depends on properties of the brain and of the sensory system that evolved for other reasons.

In other places, MSH appeared to argue for a stricter requirement, demanding that the response evolved specifically as a response to the signal. Call this the *specialised response interpretation* of the selected response requirement. This is the interpretation endorsed by Scott-Phillips (2008), who argues that according to MSH’s definition the act or structure that is the signal must have evolved to alter the behaviour of other organisms and be “effective because the effect (the response) has evolved to be affected by the act or structure” (p. 388).

Other remarks by MSH support this interpretation as well. They write that camouflage is not a signal because it lacks an evolved response (MSH, 2003, p. 5). Yet, there is an evolved response to being exposed to a camouflaged prey in the sense that there is a response that depends on evolved properties of the brain and sense organs of the predator. This is the response of *ignoring the camouflaged prey*, interpreted in light of stored sensory experiences as an inedible feature of the environment. What is missing in camouflage is a response evolved specifically with respect to the act of camouflage. Lack of specificity is due to the fact that camouflaged preys cannot be detected, and consequently cannot be responded to as camouflaged prey.

Keeping in mind that there are two possible interpretations of the selected response requirement, let us confront anew the question of whether responses to coercive signals evolved. Consider a confrontation between two stags over a contested resource. A weaker stag keeps being pushed backwards by a stronger stag. This goes on for a while, until the weaker stag adopts behavioural responses to the negative happening to which he is being subjected, namely being pushed. In the short term, the response may be to give up on the contested resource. In the medium and long term, the response may be to accept a more submissive position in the social hierarchy, and avoid further confrontations with the stronger stag.

These responses to being pushed probably explain why pushing was selected for: it is an effective means of getting contested resources, acquiring social dominance and avoiding future conflicts. These responses quite clearly depend on evolved properties of the brain and sense organs of the coerced, in the same sense in which retreating when faced by the roar of another male depends on evolved properties of the brain and sense organs of the signal recipient. Furthermore, they arguably are responses evolved *specifically* to the happening of being coerced. It seems reasonable to posit evolutionary pressures selecting in favour of organisms that take being coerced as a sign of a competitor's superior strength, and change their future behaviour towards that stronger competitor accordingly.

If this is right, coercive behaviours qualify as signals on both the generalised response interpretation and the specialised response interpretation. They alter what organisms do as a result of being coerced, they evolved at least in part because of that effect, and they are effective because the receiver's response has also evolved. But any definition of animal signalling that counts coercive behaviours as signals is too broad.

Coercion is not a solitary problem. As noted by West *et al*. (2007), MSH's "definition of a signal does not exclude actions that operate because of their substantive effects rather than their information content, so for example, it could include reciprocity, where cooperation is conditional upon the cooperative behaviour of others" (p. 419).

In cases of reciprocity, actors take turns in benefiting each other. In each interaction, the giver produces a positive happening for the receiver (e.g. being groomed). If we only looked at this aspect, reciprocal behaviours would not qualify as signals because they would fail the *specialised behaviour influencing requirement*. Being the recipient of a grooming behaviour is not something an organism *does*, any more than being pushed is something an organism does. But, as in the case of coercive behaviours, we need to broaden our focus to *behavioural responses* to being groomed. These include *reciprocating* the grooming act at a later time.

It follows that grooming behaviours alter the behaviour of another individual, and presumably evolved to influence the recipient's behaviour towards reciprocation, because this is the main expected payoff of an otherwise costly activity. Finally, grooming behaviours appear to be effective because the receiver's response to the behaviour has also evolved. This is true both in the sense that the response depends on evolved properties of the brain and sensory system of the groomed, and in the sense that the response – reciprocating a positive happening – evolved specifically as a response to earlier grooming behaviours.[15]

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[15] Scott-Phillips (2008) has argued that the response to a cooperative act in a reciprocating interaction evolved, but not specifically as a response to the cooperative act. If so, the counterexample constituted by reciprocating behaviours would only apply to the generalised response interpretation of the selected response requirement. To illustrate Scott-Phillips' counterargument, let us consider the case of reciprocal grooming, in

The troubles with MSH's definition are not yet over. Besides being too broad, such definition is too narrow (at least under the specialised response interpretation). Consider a case of deception such as the one constituted by the dangling of lures by the anglerfish. These lures are worm-like objects designed to attract preys. The problem is that, even though the anglerfish lure alters the behaviour of other organisms and evolved because of that effect, what makes it effective is not that the receiver's response has evolved to be affected specifically by the lure. The receiver's response to the anglerfish lure, namely approaching it and trying to eat it, is maladaptive, as it leads to the receiver's death.

On the other hand, it is a response that depends on evolved properties of the brain and sense organs of the receiver. In light of stored sensory experiences, the prey responds to the anglerfish lure as an actual worm, from which it is visually indistinguishable. Since there are many fewer anglerfish lures than actual worms, evolutionary pressures preserve approaching responses to worm-like objects, which usually lead to the eating of worms. But, in the same way that the response to a camouflaged prey did not evolve specifically to the camouflaged prey, the response to an angler lure did not evolve specifically to the angler lure. It follows that angler lures are incorrectly diagnosed as non-signals on the specialised response interpretation, and correctly diagnosed as signals on the generalised response interpretation.

The three problem cases I have considered so far – coercion, reciprocation and deception – can be solved if we conceptualise signals as information-mediated influencers. On the view I am proposing, a signal must be specialised for *influencing recipients by carrying information to them*. Given my definition of predictive information, this boils down to influencing recipients by changing the probabilities of states of affairs relevant to their decision-making. Coercive

which two partners take turns in grooming each other. If my response to being groomed had evolved to be affected by the grooming, he claims, the response would have to be selected in order "to reward the other participant's cooperation" (p. 390). However, the response to the grooming is not selected for this reason, but rather "to induce the other participant into a further act of altruism" (p. 390). So my response to being groomed did not evolve "to be affected by the signal" (p. 390). This argument is not persuasive. It is an arbitrary assumption that my response to grooming would have to consist in a 'reward to cooperation' in order to properly count as having evolved to be affected by grooming. Even under the specialised response interpretation, MSH's definition only demands that my response evolved as a response to your act of grooming, rather than as a response to something else. No boundaries are set on the reasons why it was selected, as long as it was selected specifically as a response to the grooming. I conclude that my grooming you is a signal by the lights of MSH's definition also on the specialised response interpretation. It is an act that alters your behaviour by making you inclined to groom me in the future, it evolved because it has that effect, and it is effective because your response to my grooming has also specifically evolved as a way to alter my behaviour by making me inclined to groom you again in the future.

and reciprocal behaviours are instead specialised for influencing recipients by other means, namely the production of, respectively, negative and positive happenings through mechanical interaction.[16]

This distinction explains why communication is, as Dawkins and Krebs (1978) noted, a good energetic bargain. Instead of recruiting one's own muscle power to bring about positive or negative happenings, communicators exploit the muscle power of another to their advantage. For instance, instead of physically "roll[ing] a female along the ground and into his burrow' (coercion), a male cricket can deliver information through a song (signalling) and "the female comes to him under her own power" (p. 282).

Requiring that information transfer mediates influence solves the problem of deceptive predation as well. As we have seen, anglerfish lures do not count as signals on the specialised response interpretation of MSH's definition (they do on the generalised response interpretation). But they qualify as signals if signals are acts or structures specialised for influencing the behaviour of another individual by means of information transfer. This is because worm-like objects carry (predictive) information about the presence of worms.

As I have argued in Section 2.2, signals carry information by changing the probability of what they are about. Given the relative frequency of worm-like objects that are actual worms (many) and worm-like objects that are anglerfish lures (few), the appearance of a worm-like object significantly increases the probability that a worm is present. This is how angler lures manage to exert their influence on signal recipients: they affect their decisions by raising the probability that a worm is present.

A critic may object that worm-like objects do not carry information about worms unless worms are present, from which it follows that worm-like objects that are anglerfish lures do not carry information about worms. This would reveal a confusion about the concept of information. If the ability of a signal to carry information about a given state of affairs amounts to the ability of the signal to change the probability of that state of affairs, the signal carries such information whether or not the state of affairs obtains. An event's failure to obtain is compatible with the reception of information about its obtaining, just like the claim that the probability that o is G is high is compatible with the claim that o is not G. No valid inference rules take us from claims about

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[16] Being subjected to a positive and negative happening also carries information (e.g. my opponent is stronger) that will be factored into the future decision-making process of the recipient. This information, however, is not what the coercive or reciprocating act is specialised in transferring, but a by-product of the happenings that the coercive or reciprocating act is specialised in producing through mechanical interaction. I thank an anonymous referee for raising this issue.

the transmission of information to claims about how things turn out to be (Scarantino & Piccinini, 2010).

I conclude that any extensionally adequate and scientifically fruitful definition of animal communication should conceptualise signalling as a specialised, information-mediated form of influencing. A systematic discussion of how a definition of this sort should be formulated, and a consideration of possible objections to it, will have to wait for another paper.

2.6 Conclusion

Information-based accounts have suggested that the evolutionary point of signalling is to transfer information. Influence theorists have rejected this view, arguing that the point of signalling must be to influence other organisms to one's advantage. However, they have assumed that it is possible to define signals in an information-free fashion, using only the notions of influence and selection. I have argued that even the most sophisticated information-free influence-based definition currently on offer faces significant counter-examples. The way to address them, I concluded, is not to fine-tune information-free accounts, but rather to conceptualise signals as acts or structures specialised for influencing by means of information transfer. This proposal combines information-based and influence-based approaches, which differ more in emphasis than in substance. Bringing both information and influence to the foreground in the definition of animal communication will allow us to combine the insights of the two research programmes into a theoretically richer hybrid.

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