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The Content of Animal Signals

Ulrich Stegmann

Animal signals are usually defined as structures or behaviors that evolved in order to carry information about the sender or the environment. They are taken to represent or indicate things; they have some kind of ‘content.’ But the nature of that content or information is not well understood. Most researchers of animal communication gravitate towards quantitative information concepts when pressed, but some regard information as awkward baggage that had better be jettisoned. In philosophy, animal signals have mostly figured as foil for discussing human language or as occasional examples in naturalistic accounts of information and representation. They became the subject of focused inquiries only fairly recently.

This chapter surveys current views about the content of animal signals. The views are drawn from both the ethological and the philosophical literature. Some of them have not been explicitly articulated before, especially the views in animal behavior studies. My formulations are therefore also attempts to explicate them. For simplicity, I formulate them in terms of necessary and sufficient conditions and presuppose that certain behaviors mean/indicate something in the first place. This allows focusing on what makes a signal mean/indicate one thing *rather* than another (i.e. the conditions for content determination).

From human communication to animal signals

Human linguistic communication is usually understood in broadly Gricean terms. On this view, linguistic communication involves not only sentences and their meanings, but also complex mental states, especially intentions to communicate and the ability to attribute mental states to others. In

addition, linguistic communication tends to serve as a general paradigm for communication and therefore often informs views on animals. Accordingly, genuine communication in animals is sometimes taken to require communicative intentions and mental state attributions; for otherwise signals seem little more than automatic manifestations of affective states (Dennett 1983). But Gricean communication demands cognitive sophistication. Some philosophers therefore distinguish between strong, Gricean communication and communication in a weak sense, as information transfer. Animal communication is then regarded as an instance of the latter, in which certain behaviors and structures merely have the biological function to convey information (e.g. Bennett 1976; Green 2007).

The distinction between Gricean communication and information transfer is useful. But it should not be confused with the claim that human and animal communication diverge neatly. First, even if communicative intentions are unnecessary, animal receivers may need mental representations in order to decode signal content (Tetzlaff and Rey 2009) or motivate action (Rescorla 2013). Second, the general absence in animals of mental abilities required for Gricean communication is contested. Gestural communication in many non-human primates, for instance, is under the sender's volitional control (Pika et al. 2007) and conveys a range of meanings (Hobaiter and Byrne 2014). Evidence for control over auditory signal production is mixed (e.g. Fedurek and Slocombe 2011; Schel et al. 2013). An even more complex picture emerges with respect to mental state attributions (e.g. Fedurek and Slocombe 2011; Andrews 2012; Keefner 2016).

Irrespective of these complications, the "signaling model" (Green 2007) chimes with the dominant view in animal behavior studies. On this view, animals communicate by conveying information from senders to receivers, with signals as the physical vehicles by which information is conveyed, and receivers acting on the basis of the information received (e.g. Bradbury and Vehrencamp 2011). The waggle dance of honeybees, for example, does not simply elicit receiver responses. Instead, the dance conveys specific information about the location of a resource to recruits, which then depart in that direction *because* they have been so informed. The informational view of animal communication is

entrenched in contemporary animal behavior studies: signals are routinely defined in terms of information (Otte, D. 1974/pe.g. ;), several classifications of signals are based on their information content,¹ and the evolutionary origin and maintenance of signaling systems is taken to hinge on signals conveying (true) information.²

Yet, what is information supposed to be in this context? Some researchers are explicit in asserting that a signal carries information in the sense that it is *about something* or *has content*, and must therefore be distinguished from information in the quantitative sense (e.g. Halliday 1983). But such characterizations are too vague and abstract for some critics of the information view (e.g. Rendall et al. 2009). Moreover, there exists no general and uncontroversial notion of content or information that one could simply apply to animal signals. The informational edifice therefore rests on poorly understood foundations.

Signal content in the ethological literature

In the ethological literature, the term “information” is often used interchangeably with what receivers come to know, infer or predict when perceiving a signal (e.g. Seyfarth et al. 2010). And acquiring knowledge from signals is often described as reducing a receiver’s uncertainty (Wiley 1983; Seyfarth and Cheney 2003; Bergstrom and Rosvall 2011; Wheeler et al. 2011). These practices suggest a first family of views about the content (X) of animal signals (S):

[1] S 's content is X iff R infers/predicts/comes to know/becomes more confident that X , given S

Consider a female firefly (R) perceiving a male’s light pulse (S). According to [1], the information carried by S depends on what the female infers from it. Plausibly she infers from S that there is a male conspecific willing to mate. The phrase following the *that*-clause is therefore the content of S . Encouragingly, this is just the kind of content that ethologists have actually attributed to male light

pulses: “Here I am in time and space, a sexually mature male of species X that is ready to mate” (Lloyd 1966, p. 69).

However, [1] appeals to several distinct processes. Becoming more confident about X , for instance, does not imply knowing that X is true. Also, inferring and predicting is sometimes taken to include automatic responses based on reflexive associations and evolved dispositions (e.g. Krebs and Dawkins 1984). So, [1] is much too vague to specify the content of animal signals. And simply settling on one of the processes will not do. A principled argument is required as to why one of the processes, rather than some other, qualifies as determining a signal’s content.

There is evidence that some signals elicit mental representations in receivers. Rather than triggering a reflexive response, these so-called “representational” (Evans and Evans 2007) or “conceptual” signals (Zuberbühler et al. 1999) are assumed to have their effects on receivers via internal representations. Some authors go a step further and distinguish informational from non-informational interactions along these lines. Accordingly, a structure or behavior carries information *only* if it elicits a thought or mental image in the receiver, not if it triggers a reflexive response. The content of signals then tends to be identified with the content of the internal representation (Maynard Smith and Harper 2003; Seyfarth and Cheney 2003). Interestingly, the critics of the informational view have also sought to distinguish between informational and non-informational interactions and they come to broadly similar conclusions: interactions are informational if the receiver response relies on cortical as opposed to non-cortical processing (Rendall et al. 2009), or on cognitive as opposed to non-cognitive processing (Owings and Morton 1998). In short, at least some of the proponents and opponents of the information view agree to the extent that information is exchanged only if the receiver processes what it perceives by means of a higher-order mechanism. This suggests another group of views about content:

[2] S ’s content is X iff S elicits in R a cognitive or cortical representation of X /thought of X /mental image of X

Again, [2] offers several distinct higher-order mechanisms (e.g. cognitive processing does not imply mental imagery) and it is unclear which of these might determine signal content. Furthermore, organisms relying on lower-order mechanisms will not qualify as exchanging information. And this implication does not sit well with the usual understanding of communication in animal behavior studies.

Faced with these challenges it may be tempting to seek refuge in quantitative frameworks. Two quantities, entropy and mutual information, have become particularly influential in ethology (e.g. Halliday 1983; Seyfarth et al. 2010; Wheeler et al. 2011). Shannon entropy is a measure of the number of different states, and their probabilities, that a system can assume. Systems with many, equally possible states (e.g. the six sides of fair dice) are associated with a higher degree of uncertainty about the system's current state than systems with few possible states, of which one is very likely (e.g. bank vaults being locked/unlocked). Mutual information captures the statistical association between two such systems. In the 1950s and 60s, several studies estimated the mutual information between signals and receiver responses (see Halliday 1983). However, since signals are not normally taken to be about their effects on receivers, this measure ("transmitted information", Wiley 1983) cannot capture a signal's information content. Closer to the target is the mutual information between signals and the states they are about ("broadcast information", Wiley 1983). Hence the following idea:

[3] S 's content is X iff S has non-zero mutual information with X

However, Shannon's quantities are not equivalent to (or a measure of) information in the colloquial sense of content, a point acknowledged by several early ethologists. One reason is that the quantities average across all the states a system can have, whereas content in the colloquial sense is not an average (Dretske 1981). Another reason is that S 's reducing R 's uncertainty about X is a 3-term

relation (involving S , R , and X), whereas mutual information is only a 2-term relation between S and X .

Nowadays the preferred quantitative framework in animal behavior studies is statistical decision theory (Bradbury and Vehrencamp 2011). Its basic idea is that animals can use current perceptions to update their prior knowledge about events. Background knowledge stems from earlier experiences and/or evolutionary history. SDT employs Bayes' theorem to derive posterior probabilities. The difference between posterior and prior probabilities is understood as measuring the animal's uncertainty reduction about the state whose probability is being updated. The following account of content suggests itself:

[4] S 's content is X iff S updates R 's expectation about X

Bayesian probabilities are traditionally understood as degrees of belief. This raises the question of the nature of beliefs in, say, invertebrates and organisms lacking nervous systems. Perhaps to avoid these issues, SDT remains explicitly neutral about the mechanisms of updating (e.g. Bradbury and Vehrencamp 2011). But this strategy raises another problem. If SDT is simply employed as a predictive tool, then it justifies construing S merely *as if* having content.³

Signal content as natural information

Philosophers tend to regard the content of animal signals as an instance of either natural or semantic information.⁴ These two types of information are distinguished with respect to whether or not they allow for having false contents. Falsity requires that something can carry the information that p despite it's being the case that not- p . For instance, the belief that it is Friday carries the information that *it is Friday*, which may or may not be true (semantic information). Tree rings, by contrast, are standard

examples of natural information. Six tree rings indicate that the tree is six years old, because the tree would normally not have six rings unless it actually was six years old.

Just as tree rings are reliably caused by an annual period of slow growth, animal signals are often produced reliably in response to certain events or objects, e.g. predators. And so, just as tree rings indicate age, animal signals indicate various events or objects. This core idea has been developed in different ways. Some authors rely on strong versions of natural information, according to which one state indicates another only if the first could not obtain without the second; a signal thus guarantees that the indicated state obtains (Dretske 1981; Adams and Beighley 2013). But most commentators believe that such strict relations rarely obtain. Another group of theories therefore allow that a state can carry information about another even if the first can obtain without the second (Millikan 2004; Shea 2007; Skyrms 2010). A well-articulated theory of this sort is defended by Scarantino (2015).

A centerpiece of Scarantino's theory of natural information is that one state carries information about another when the first makes the second more likely (or less likely):

“Incremental Natural Information (INI): r 's being G carries incremental natural information about s 's being F relative to background data d if and only if $p(s \text{ is } F | r \text{ is } G \ \& \ d) \neq p(s \text{ is } F | d)$ ”
(Scarantino 2015)

The key idea can be put as follows. Entity s has a certain prior probability of being F given some background data. Then r is observed to be G . This fact may or may not make a difference as to whether s is F . If it does make a difference to the probability of s 's being F (by making it more likely, or less likely, that s is F), then r 's being G carries information about s 's being F . Notice that the information content of r 's being G is not (only) that s is F . This is because the occurrence of a state of affairs usually affects the probabilities of many states rather than just one. Scarantino's formal definition of information content is too complex to reproduce here; suffice it to say that it includes

three features: the identity of the states whose probabilities are changed, the amount of change, and their probabilities after the change. Scarantino holds that animal signals carry information in this sense. For instance, for vervet monkeys there is always a certain background probability that an eagle approaches. But hearing an eagle-alarm call makes that event much more likely. Eagle alarm-calls therefore carry incremental information about the presence of eagles. Hence:

[5] S 's content is X iff S changes the probability of X

Animal signals *do* change the probabilities of other states. However, I am not convinced that this is the kind of information which scientists actually attribute to signals and which figures in their explanations and predictions (Stegmann 2015). First, INI-contents are much broader than the contents attributed by ethologists. For instance, the content ethologists attribute to the eagle-alarm calls of vervet monkeys is that an eagle is approaching. But their INI-content includes an array of additional states, e.g. the eagle having been detected, the eagle's foraging success being reduced, the caller interrupting foraging, the receiver taking evasive action, and so on.

Second, signals carry weak natural information if they are sometimes produced in the absence of the states whose probabilities they change. But are signal *tokens* produced in the absence of the correlated state informative? If yes, then they would appear to carry the information that p despite not- p and, hence, false information. This would contradict the widely held view that natural information cannot be false (e.g. Dretske 1981; Millikan 2004; Adams and Beighley 2013). One might claim, instead, that the information is not actually p alone, but rather a disjunction of all states causing or correlating with the signal, i.e. $\langle p \text{ or } q \text{ or } \dots \rangle$. This disjunctive content is true even if in a particular instance p does not obtain (Adams and Beighley 2013). This move, however, spells trouble for signals whose contents are taken to be specific (see above). A third option is to deny that such tokens carry any natural information (Millikan 2004). But in that case carrying information cannot merely be a

matter of being an instance of a probabilistically related type, contradicting the very notion of weak natural information (Stegmann 2015). Furthermore, this option is at odds with the ethological practice of classifying such signals as indicating falsely or “dishonestly” (e.g. Maynard Smith and Harper 2003).

Let us step back from these objections and take a broader look. It has been argued that there exists a group of signals that do more than simply carry natural information. So-called “expressive behaviors” (Bar-On and Green 2010) are designed to “express” or “show” an animal’s affective states. Affective states are directed towards events or objects, which are their non-propositional intentional objects (e.g. excitement *about* food). Expressive behaviors are said to carry natural information about the things that reliably cause them. But they are also “precursor[s] of linguistic behavior” (Bar-On and Green 2010, p. 104), both because they express states with intentional objects and because they are designed to elicit appropriate receiver responses. One might therefore construe expressive behaviors as having a kind of content:

[6] *S*’s content is *X* if *S* is designed to express *X*, where *X* = <affective state directed at non-propositional intentional object>

On this reading, the content of an (expressive) signal is a certain mental state and its intentional object. In a similar vein, Proust (2016) suggests that mental states called “affordance-sensings” mediate the exchange of animal signals. Affordances are, roughly, the behavioral opportunities that a situation allows or requires. Signals convey affordances; they do not refer to states in the world.

It may be objected that even signals expressing affective states can carry propositional content. Arguably, one must distinguish between (1) signal production, which is the expression of an affective state, and (2) the product (signal) itself, which could have propositional content. McAninsh et al. (2009) make this point and argue that at least some animal signals are of this kind. This brings us to

theories according to which the content of animal signals is an instance of semantic information or, equivalently, representational content.

Signal content as semantic information

Dretske (1988) proposed a general theory of representational content, according to which a state represents another just in case it has the function to carry natural information about the other. Hence:

[7] S 's content is X iff S has the biological function to carry natural information about X

The appeal to function avoids the ubiquity worry raised against probabilistic accounts. But other challenges emerge. One is that many signals do not guarantee that the represented state obtains or even make it likely. Furthermore, some signals evolved in order to “deceive” receivers, i.e. to represent falsehoods, and [6] cannot account for their content. Predatory fireflies, for instance, mimic the light pulses sent by females of other species and consequently lure males of those species to their deaths. For the predators' signals to falsely represent the presence of females, they would need to have evolved in order to indicate the presence of females. But they systematically fail to achieve that function. So probably their function is to mislead males. But then they do not represent females.

While Dretske's (1988) account ties content exclusively to the signal producer, Millikan's account (2004) includes the receiver. *Signal-producing* mechanisms (in the sender) evolved in order to issue signals in response to certain conditions, so that variations in the signals' physical features map to variations in the conditions. The time and location of a beaver's tail splash, for example, correspond to present danger, just as the specific features of a bee's waggle dance correspond to a certain location relative to the hive. *Signal-consuming* mechanisms (in the receiver) evolved to respond with behaviors that benefit both sender and receiver, such as taking cover or flying to the signaled location. Another important component of Millikan's theory are “normal conditions”. This is a technical term for the

states of affairs that obtain when mechanisms achieve their functions in the way that explains the mechanisms' evolution, rather by accidental means. For instance, the normal condition of the consuming mechanism of beaver tail-splashes is the presence of danger, because this co-occurrence obtains when the mechanism achieves its function in the way that explains its evolution. Recall that this co-occurrence is also the function of the tail-splash producing mechanisms. So, the normal condition of a consuming mechanism is that the producing mechanism achieves its function, and vice versa; signal-producing and -consuming devices must "cooperate" in this manner. With these elements in place, Millikan identifies representational content as the state of affairs to which the signal evolved to correspond and whose co-occurrence with the signal is the normal condition of the consuming device.

[8] *S*'s content is *X* iff (1) *X* is the state to which *S* evolved to correspond and (2) *S*'s co-occurrence with *X* is the normal condition of the consuming mechanism

Millikan's theory reconstructs the specificity of many signals. For instance, in the case of the light pulses of male fireflies, *X* is the presence of a male firefly ready to mate. [8] also accounts for the possibility that signals can be true or false; they are true when the producing-mechanism achieves its function and false when it does not. Hence, some authors are sympathetic to this account (Allen and Saidel 1998; Godfrey-Smith 2013; Artiga 2014).

Deceptive signals remain problematic, however. The producing mechanism of the predatory firefly achieves its function when it produces a mimicking signal in the presence of itself, the predator. But the co-occurrence of female-type light pulses with a predator is not the normal condition of the males' consuming mechanism; it is not the kind of circumstance under which males' responses resulted in matings. The predators' light pulses therefore do not belong to a cooperative system, and hence lack representational content (Stegmann 2009). However, Artiga (2014) maintains that the light pulses can

be individuated so that they do belong to a cooperative system. Another move is to accept the argument's conclusion but maintain that it is unproblematic: essentially, males just mistake content-free mimics for meaningful models (Adams and Beighley 2013; Artiga 2014).

I prefer to abandon Millikan's cooperation requirement and simply let receivers determine signal content (Stegmann 2009; 2013). Here is my proposal:

[9] *S*'s content is *X* iff (1) *S* elicits a response *B* in a receiver and (2) the receiver acquired its *B*-disposition due to past *S*-tokens that co-occurred with *X*s

where *S* is a token entity; *B* may or may not be a behavioral response; and receivers can acquire responses through learning and/or evolution. Consider firefly signals. A female-type light pulse (*S*) prompts a male to approach (*B*), and the male acquired this disposition due to an evolutionary process in which past light pulses of this kind co-occurred with conspecific females (*X*). The content of the light pulse is therefore the presence of a conspecific female. Crucially, the light pulse has this content independently of whether it was produced by a conspecific female or by a predator. This is because the content is determined only by a historical fact about the receiver. It is worth noting that the co-occurrence of *S* and *X* can be a correlation, as in this example, or a one-off coincidence, as in one-trial learning.

One implication of [9] is that signals have specific contents only in virtue of, and relative to, certain receivers. This implication explains why the same signal can mean different things to different receivers { {296 Smith,WJ. 1977; 555 Stegmann,Ulrich E. 2009} } and renders it applicable to *cues*. Furthermore, content attributions become testable. To claim that (1) 'this female-type light pulse *signals* the presence of a female' is equivalent to claiming that (2) 'the presence of a female is the *acquisition condition* of the receiver's response'. Whether or not the latter claim is true can be tested.

Finally, [9] renders content attributions explanatory. For example, the presence of females (the acquisition condition/content) explains why male fireflies tend to approach female-type light pulses.

Despite these attractions, [9] faces challenges like the demarcation of acquisition conditions and complications due to stimulus categorizations by receivers. It is also vulnerable to some of the objections raised against Millikan's theory. Among the latter are the counter-intuitive consequences when signals are not triggered by S , but rather by a state Y that shares a common cause with S (Godfrey-Smith 2013), or the view that representational content achieves no explanatory gain over and above correlations (as Rescorla 2013, has argued with respect to bees). Nevertheless, I believe that [9] offers the best prospects for developing a successful theory of signal content.

Notes

² For instance, the classification based on whether the information is about the sender or a third party (e.g. Halliday 1983; Krebs and Dawkins 1984), or the classification distinguishing between “indices”, “icons”, and “symbols” (Maynard Smith and Harper 2003).

³ If signals carried (mostly) false information, then responding to them would not be an evolutionarily stable strategy for receivers (Maynard Smith and Harper 2003).

⁴ Kristin Andrews (pers. comm.) notes that one might understand probabilities in terms of “degrees of cognitive representations”, while remaining neutral about whether those cognitive representations are beliefs.

⁵ The distinction originated with Grice's distinction between “natural” and “non-natural meaning”.

Further Reading

An illuminating, early philosophical treatment of animal communication is J. Bennett, *Linguistic Behaviour* (Cambridge: Cambridge University Press, 1976), §62. According to R. G. Millikan, *The Varieties of Meaning* (Cambridge, MA: MIT Press, 2004), animal signals have representational content. For A. Scarantino, “Information as a Probabilistic Difference Maker,” *Australasian Journal of Philosophy* 93 (2015): 419-43, they carry natural information. J. Bradbury & S. Vehrencamp, *Principles of Animal Communication* (Sunderland, MA: Sinauer, 2011) is the principal textbook in the information tradition. Contributors from different fields discuss informational and non-informational accounts in U. Stegmann (ed.), *Animal Communication Theory: Information and Influence* (Cambridge: Cambridge University Press, 2013).

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