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## Information and uncertainty in meerkats and monkeys

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### 13.1 Introduction

The papers published in 1980 by Robert Seyfarth, Dorothy Cheney and Peter Marler on the alarm calls of vervet monkeys were instant classics. In a short paper in *Science* (Seyfarth *et al.*, 1980a) and the more detailed companion piece in *Animal Behaviour* (Seyfarth *et al.*, 1980b), they described experiments that Seyfarth and Cheney had conducted in Kenya's Amboseli National Park. They played pre-recorded vervet monkey vocalisations from loudspeakers hidden in bushes, to test the reactions of the monkeys who were within earshot. They used the different "alarm calls" that are commonly produced when vervet monkeys detect predatory eagles, leopards and snakes, and observed the vervets responding in predator-appropriate ways to the three kinds of calls. With Marler, their postdoctoral advisor who had initially suggested the experiments, they argued that these differential responses to the alarm calls showed that monkeys hearing these calls obtain specific information about the type of predator, not just the emotional or arousal state of the signaller. They claimed that these calls are thus an example of 'referential communication' in a non-human primate.

The vervet alarm calls have achieved iconic status, even among those philosophers who know little about the experimental details or scientific context in which the experiments were developed. Among biologists, the research has spawned a veritable industry that employs playback methods to investigate 'referential communication' in a variety of different species: primates, meerkats, prairie dogs, domesticated chickens and so on. The use of the playbacks in such experiments is now itself the subject of serious study within history and

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philosophy of science (Radick, 2007). If there is one example of a successful research programme involving scientists who accept the label of ‘cognitive ethologist’ for themselves, it is the investigation of referential communication.

From an evolutionary point of view, the systems of alarm calls and responses found in various species can sometimes be understood in terms of kin selection. Individuals living together in groups often comprise a network of genetically related individuals, and insofar as the predator-appropriate responses of receivers decrease the mortality of related individuals hearing the calls, this increases inclusive fitness of the signallers even if they incur a potential cost by attracting the attention of predators to themselves. From a cognitive point of view, many ethologists have been inclined to say that such calls inform other group members about the presence of predators. However, and as other chapters in this volume discuss, this framing of animal communication in terms of information has proven controversial.

The most vociferous criticisms are to be found in a series of papers by Michael Owren, Drew Rendall and colleagues (e.g. Rendall & Owren, 2002; Rendall, Owren & Ryan, 2009; Owren, Rendall & Ryan, 2010). They argue that the notion of ‘information’ as used by ethologists imports metaphors from human language that are not scientifically grounded in the facts about animal communication. They assert that it is a mistake to try to understand more primitive forms of animal communication using features derived from more recently evolved human language. As an alternative, they suggest that a more fruitful approach would be to focus on the ways in which physical characteristics of signals, such as pitch, duration and intensity, activate emotion-related or motivational systems in receivers. Their view is summarised in the title of Owren, Rendall and Ryan’s 2010 paper, “Redefining animal signaling: influence versus information in communication”, urging ethologists to focus on the *influence* that signallers have on receivers (they prefer ‘perceivers’) rather than *information* conveyed from one to the other.

Seyfarth, Cheney and four co-authors have responded to this challenge with a paper titled ‘The central importance of information in studies of animal communication’ (Seyfarth *et al.*, 2010), in which they accuse their opponents of attacking a straw man. However, their response fails to deal with one of the main complaints raised by Owren *et al.* (2010), namely that the notion that animal signals convey or contain ‘information’ is not appropriately connected by the cognitive ethologists to the quantitative measure of information developed by Shannon and based in probability theory. Seyfarth *et al.* (2010) include a very brief section, consisting of exactly one paragraph, in which they refer to Shannon (1948) and Wiener (1961) to ground their use of the term ‘information’ as ‘reduction of uncertainty’. They mention ‘reduction of uncertainty’

only once more – in the immediately following paragraph that heads the next section – while continuing to use the term ‘information’ throughout the rest of the paper without any further reference to probabilities. It is precisely this kind of pro forma mention of Shannon’s definition that leads the critics to complain about failure to properly tie the notion of information in animal communication to Shannon’s probabilistic theory of communication. As Adams and Beighley (Ch. 17 of this volume) put it, “The complaint is that people cite Shannon and Weaver (1949) and then move on without explanation.”

There is both a practical point and a definitional point here. On the practical side, even though quantitative analyses of the information in animal communication have sometimes been attempted – the first effort in this direction being an analysis of honeybee communication by Haldane and Spurway (1954) – the assumptions about receiver perception and signal measurement that are required for absolute quantities to be calculated may be hard to verify (e.g. Beecher, 1989). On the definitional side, is the question of how (indeed, whether) to connect the probabilistic notion of ‘reduction of uncertainty’ to the notion of specific informational content. Owren *et al.* quote Weaver (from Shannon & Weaver, 1949, p. 99) to support their claim that “meaning and significance are quite different from Shannon information” (Owren *et al.*, 2010, p. 761). They also cite Dretske (1981) as supporting “the originators’ admonition to separate information from meaning” and they go on to assert that Shannon’s concept of information is “incommensurate” with the approach adopted by animal communication researchers. Philosophers familiar with Dretske’s (1981) book may be somewhat puzzled by this. Distinctions do not imply incommensurability. Although Dretske does not equate semantic content to information, a major effort of the book is nevertheless to explicate content in information-theoretic terms. My main goal in this chapter, however, is not to set the record straight about Dretske’s account of intentional content (but see Allen, 1995 for a comparative review of philosophical accounts, including Dretske’s).

In this chapter, I argue that *information* versus *influence* presents a false dichotomy for the study of animal communication. The information eliminativists’ argument that ethology would be better off without a notion of information is based on inordinate concern for what Owren *et al.* (2010, p. 766) describe as the “over-complicated accounts of perceiver processing” that they associate with the informational view of animal communication. The allegedly less complicated ‘influence’ view of communication may only seem less complicated when certain complexities of animal communication are wilfully ignored. Shannon (1956) cautioned against jumping on “the bandwagon” of information

theory whose basic results, he wrote, were “aimed in a very specific direction . . . that is not necessarily relevant to such fields as psychology, economics, and other social sciences” (p. 3). Nevertheless, he went on to say that he personally believed that “many of the concepts of information theory would prove useful in these other fields” – but he insisted that the utility of what is essentially a deductive, mathematical theory would need to be established experimentally. After surveying the debate in more detail, I discuss two experiments illustrating the utility of Shannon’s approach.

### 13.2 Information overload?

The pair of papers contributing to the debate among the ethologists in 2010 represent something of an in-house dispute among the academic progeny of Peter Marler. Many of the major protagonists (Robert Seyfarth, Dorothy Cheney, Marc Hauser, Chris Evans, Klaus Zuberbühler, Julia Fischer, Drew Rendall, Michael Owren etc.) were directly advised by Marler or by one of his advisees. Others in this debate, such as Don Owings, were colleagues of Marler at the University of California, Davis, or otherwise connected to the UC Davis department. Michael Owren was Cheney and Seyfarth’s first postdoctoral advisee, working at UC Davis, and Drew Rendall, who did his PhD at UC Davis also later became their postdoctoral advisee.

Although Shannon’s account of information played a role in Marler’s thinking about animal communication, it is by no means the sole starting point. The debate in which Marler was engaged can be framed as follows (I owe the following list to my student Robert Rose; see also Radick, 2007):

- (1) Haldane and Spurway’s (1954) information-theoretic analysis of the honeybee waggle dance as carrying 5 bits of information of which 2.5 bits on average are picked up by the honeybee audience.
- (2) The rejection by Lorenz and Tinbergen (and Haldane) of a ‘mentalist’ or ‘semantic’ reading of claims about information, instead seeing such signals as ‘triggers’ of automatic responses. (See also Adams and Beighley, Ch. 17 of this volume, for a similar characterisation of the role of ‘information’ in analysing animal communication.)
- (3) Marler’s reading of Peircean semiotic theory (see Peirce, 1935), and descendants thereof, specifically Ogden and Richards (1923), Morris (1946) and Cherry (1957), according to which the triadic relationship among *object*, *sign* and *interpretant* is irreducible to binary relationships. Marler combines this with Morris’ operationalised notion of ‘interpretant’ in terms of behavioural dispositions in the receiver.

Marler also accepts the semioticians' identification of the referent of a communicative act as the object in this triadic relationship.

- (4) Marler's following of Ogden and Richards in taking the relationships linking signs and objects to be 'imputed' – meaning that these relations are mediated by psychological agents.
- (5) The rejection by Marler (1961), following Morris (1946), of a dichotomous view of animal communication as either emotional or referential – a distinction that has its roots in Darwin (Radick, 2007). Why not both?
- (6) Marler's rejection, following Cherry (1957), of a clean distinction between 'semantics' or the study of 'meaning' of signs and 'pragmatics' or "the significance of signals to the communicants" (Marler, 1961, p. 229), at least for the purposes of studying animal communication.

Although Marler read widely in the semiotics literature, little of this shows through in the papers that established the research programme at the heart of the current dispute. However, I believe that the notion of *imputed* significance is key to seeing our way through the current thicket of ideas about information in animal communication. Of course, the idea that perceivers 'impute significance' to signals suggests the kind of cognitive sophistication that makes Owren *et al.* nervous about metaphors drawn from human language understanding. I will use some recent research on meerkats in which I had a hand to try to illustrate how cognitive capacities can be related to animal communication and studied rigorously without assuming a linguistic conception of information.

Before introducing the meerkats, let me try to be a bit more specific about the standard linguistic conception of information. (I owe much of the following paragraph to conversations with Michael Ramscar, and to his paper "Information: a theory of human communication", in preparation.) The standard model of language takes meaning to be directly encoded in words and sentences, and thus extractable by a knowledgeable hearer or reader. A knowledgeable receiver knows the lexicon which associates words with meanings (or concepts) and, if the language is a sophisticated one, the rules for assembling larger meaningful utterances from the lexical items. The dominant metaphor becomes one of message passing – a fixed message is packaged by a speaker into a predetermined code that is extracted by a competent listener. In contrast to the orthodox view, even though certain aspects of this code may be conventionalised, it is better (and more consistent with Shannon) to think of these messages as something that competent receivers must *reconstruct*. The process is closer to probabilistic reasoning than semantic lookup. I will describe the application of these ideas to a study of meerkat communication below.

### 13.3 Meerkat individuals

Meerkats are a kind of mongoose endemic to southern Africa. They live in colonies of up to 50 individuals dominated by a dominant pair, and they produce a number of distinctive vocalisations that are functionally related to different social situations and predator threats. Meerkat vocalisations are also distinguishable at the individual level, but meerkat researchers had found themselves rather stumped when it came to testing whether the meerkats themselves were capable of recognising individuals by vocal cues alone. It was hard to find any naturally occurring situations in which the identity of the signaller mattered to the meerkats, except those involving the dominant animal. A study found that subordinate animals can distinguish the calls of the dominant female from those of other females based on sound alone (Reber, 2010). However, because there is exactly one dominant female in each group it could not be determined whether this discrimination indicated only category-level recognition (dominant versus subordinate) or more fine-grained individual recognition. No difference in social response to subordinate females could be discerned.

Years ago, I had helped brainstorm the design of Dorothy Cheney and Robert Seyfarth's habituation experiments with vervet monkeys, in which they repeatedly played the calls of a single individual, habituating the others to that call, and then tested with other calls from the same individual and different individuals. They found that habituation did not transfer between alarm calls, but that habituation did transfer between acoustically distinct social contact calls from the targeted individual, suggesting meaning-based categorisation of signaller reliability (Cheney & Seyfarth, 1988). In the present context, I am willing to treat the claim that vervets categorise calls by meaning as controversial. However, because the transferred habituation was limited to calls from the same individual, it should be uncontroversial that this can only be explained if the monkeys are sensitive to individually distinctive elements of the calls.

Such experiments are difficult to carry out. Cheney and Seyfarth had been very careful to play a call from the hidden speakers only when the monkey whose call was being played back was out of sight of the others. The habituation phase is especially difficult because multiple exposures are needed but appropriate opportunities are spread over days and weeks. Nevertheless, an attempt was made by Schibler and Manser to carry out a version of Cheney and Seyfarth's 1988 unreliable signaller experiment on the meerkats. However, the meerkats showed no transfer of habituation, leading the researchers to title their paper, "The irrelevance of individual discrimination in meerkat alarm calls" (Schibler & Manser, 2007). Schibler and Manser noted that

individual discrimination might occur in some contexts, but that it was not important for the meerkats to respond differently in the specific context of this experiment.

At a meeting in Berlin in July 2010, I suggested a different approach to meerkat researchers Marta Manser and her postdoc Simon Townsend. The approach was based on violation of expectation that did not explicitly require prior habituation. The thought was this: if meerkats are able to identify individuals by their vocalisations alone and are sensitive to the direction from which a call is heard, then they ought to find it surprising if they receive evidence of a nearly instantaneous shift of location of a single individual. So, if it were possible to locate two speakers on opposite sides of a focal subject and play, in rapid succession, social contact calls from the same individual, at a time interval that was too short for the caller to have changed location, then an attentive listener ought to show some sign that this was unusual. Meerkats have a 'close' call which Manser had hypothesised to play a function in maintaining group cohesion (Manser, 1998) and that had been shown by Townsend, Hollen and Manser (2010) to be individually distinctive by acoustic analysis. The 'close' call seemed, therefore, to be a good candidate to use in this experiment. Although we did not know exactly what meerkats would do in the situation where they heard separately recorded 'close' calls from the same individual (AA' pattern), we reasoned that a different reaction to the AA' pattern versus calls from two different individuals coming from different sides (AB pattern) would show that the animals were tracking individual identity by vocal calls alone. To short-circuit an even longer story, this is indeed what Townsend found when he ran the experiment at the Kalahari Meerkat Project study site. (Yes, Meerkat Manor!) Meerkats hearing the AA' pattern with approximately 4 s separation between calls became more vigilant and were more likely to look in the direction of the second loudspeaker than those hearing the AB pattern. In the published description of this experiment we argued that it showed within-category discrimination amongst the subordinate individuals who are tracked spatially (Townsend, Allen & Manser, 2011).

It would be more succinct to say that meerkats obtain information about identity and location from the 'close' calls of group members, but because the issue of information is contested by Owren, Rendall and Ryan (Rendall *et al.*, 2009; Owren *et al.*, 2010) it is necessary in the present context to justify speaking that way. But why introduce the notion of information at all when we did not use the term in the written report? The short answer is that the language we did use, of tracking identities and locations of individuals through time, concerns information available to the hearer rather than immediate behavioural influence exerted by the caller on the perceiver. The long answer follows.



### 13.4 What meerkats impute

In our paper we argued that the experimental results “suggest that meerkats do indeed have a concept of conspecifics as ‘individuals’ recognised perceptually” (Townsend *et al.*, 2011). Our circumspection about this claim derives from a lack of a cognitive model or mechanism to explain the meerkats’ spontaneous tracking of the location of nearby individuals from moment to moment. Nor do we have any evidence pertaining to whether meerkats can integrate individual identity cues from different modalities such as sight, hearing and smell, or track individuals over the long term. The attribution of individual concepts serves as a placeholder pending further investigation of the processes and mechanisms. In the context of the present volume, nothing depends on the claim that the meerkats have individual concepts. Nevertheless, I would argue that the issues that lead some to be skeptical of animal concepts are analogous to those in the controversy about information in animal communication.

One way to make the connection is via the critique offered by Chater and Heyes (1994) of the notion of ‘concept’ in animal cognition. Similar to the complaint by Owren *et al.* that the notion of information as deployed by ethologists imports metaphors from human language, Chater and Heyes’ argument is that the notion of concept is not well defined outside the context of language users. I will not rehearse the full responses to their argument here, but in my view (elaborated in Allen, 1999; see also Newen & Bartels, 2007) the best justification for concept attribution involves the sensitivity of the animals to epistemic failure, i.e. noticing and learning from their own errors of categorisation when an expectation is violated. When categorisation seems to be going smoothly and there are no errors, the notion of a concept may seem superfluous because one can simply regard the categoriser’s response as directly driven by properties of immediate stimuli. But when things go wrong and expectations are violated, sophisticated configural learners – concept users – simultaneously update their responses not just to features of the stimulus directly involved in the event but to various related features that were absent during the violation of expectation. Contra Chater and Heyes, the use of the word ‘concept’ is meaningfully attributed even when the categorising animals do not have explicit labels (words) for their categories. When cognitive agents learn from their prediction errors about specific instances, they reconfigure the relational structure among the features relevant to the entire category, even features absent from the instance generating the error. The cognitive structures that are constructed and reorganised by discriminative learners are the concepts. And while the best discriminative learning models are associationist in flavour, this



is not your grandfather's behaviourism (Smith, 2000; also, M. Ramscar, in preparation).

The idea of multiple adjustments within a category is implicit at the core of the 'unreliable signaller' experiment of Cheney and Seyfarth (1988). The habituated group members did not just come to ignore the one individual's signal that was played repeatedly during the habituation phase of the experiment (a 'wrr'). They also came to ignore another kind of acoustically distinct call from the same individual played in the test phase (the 'chutter'). This cannot be explained without attributing some cognitive structure to the monkeys to connect wrrs to chutters. They both belong to the category of social contact calls. The change of significance of the chutters is 'imputed' insofar as nothing intrinsic to the signs themselves (the wrrs and chutters are acoustically distinct) or to the sign-object relationship suffices to explain the pattern of results without bringing the 'interpretant' – and hence the receiver's cognitive architecture – into it.

Now, it might be argued, from a behaviourist point of view, that stimulus contexts are what wrrs and chutters have in common. Both kinds of social signal tend to occur in similar contexts, allowing the animal to learn their association. Putting this in semiotic terms (but abandoning the semioticians' insistence on the irreducible ternary nature of communication), one might say that because wrrs and chutters both connect to situations involving social contact with other groups, the binary relationship between sign and contexts involving social contact (the object of communication) is sufficient to explain the receiver's transfer of habituation between the two calls. This will not do, however. Different alarm calls all connect to situations involving contact with predators, yet the monkeys did not transfer habituation between the alarm calls that were used in the experiment. Perhaps, though, predators and the corresponding alarm calls tend to occur in noticeably different contexts (bushy areas for snakes, more open spaces for eagles, for example). Even so, the monkeys would need to have learned to discriminate social contact among the contexts for alarm calls, while they learned to ignore the same contextual features surrounding calls. It is only against the background of this difference – a fact about the acquired cognitive structure of the receivers – that we can understand why the transfer of habituation occurs in some cases and not in others.

The fact that the monkeys group some sign-object relationships together but discriminate others is a fact that necessarily involves their role in imputing significance to the calls, not merely to externally given sign-object relationships. The role of their cognitive architecture goes beyond perception of the physical characteristics of the signal such as pitch and volume (the aspects of receiver psychology that Owren, Rendall and Ryan emphasise by insisting on

using ‘perceiver’ in place of ‘receiver’). It requires our attention, as theorists, to the informational properties of the signals. Of course, the calls *influence* receivers too. Receivers could hardly be informed without being influenced. But the nature of that influence fits Shannon’s conception. When monkeys cease responding to an individual’s chutters, it is not because the objective relationship between chutters and the environment has changed. The relationship of that individual’s chutters to social contact with another group is exactly the same at the end of the experiment as it was at the beginning. Only the informational entropy of the individual’s wrrs has been objectively changed (by changing the probabilistic relationship between the wrrs and social contact with another group). Nevertheless, the receivers’ expectations about chutters have changed, which is an imputed change in significance.

The violation of expectation in our meerkat experiment forces similar considerations. In normal interactions, ‘close calls’ influence perceivers’ overt behaviour rather minimally. But the very same call can have a different influence based not on anything intrinsic to the call, or to the signal–object relationship per se, but depending on an imputed significance given what information the meerkat has about the prior location of the caller. By attending to prediction errors, the meerkats learn to better predict, and in this sense understand, the world around them (cf. M. Ramscar, in preparation).

How does this connect back to Shannon? A Haldane-style calculation of the average bit rate of any single call might be possible, in principle if not in full practicality. If we start with the assumptions that in any given situation a meerkat initially has no information about the location of a fellow group member, that all relative directions are equiprobable, and that the physics of sound production and sound wave propagation provides much greater potential for identifying the source than meerkats can discriminate, then the average amount of locational information conveyed by these calls depends on the directional and distance resolution of the perceiver (how many radial sectors can be distinguished and what kind of range discrimination exists) and the amount of individual information depends on how many individuals can be discriminated. In any given situation, the amount of information actually extracted by the receiver depends on her prior information state. So, given two ‘close’ calls from the same individual in the same location, the second might provide only a small amount of new information to the receiver, which is related to reducing any uncertainty that comes from the signaller’s having moved location since the first call.

Only some very rough, back-of-the-envelope calculations are possible here. We could make an assumption about the average amount of information conveyed by a ‘close’ call by assuming something about the radial discriminability

of the signals (say 32 equal-sized sectors within the 360° range, which gives 5 bits), the range discrimination (assume just two range bands, ‘very close’ and ‘close’, for 1 bit) and the individual discrimination capabilities (say a maximal group size of 64 individuals, for another 6 bits). We could then estimate the reduction of uncertainty provided by a second call, based on the typical movement patterns of meerkats. This corresponds to the entropy (uncertainty) of a joint event  $(x, y)$  which Shannon (1948, p. 22) defined as the sum of the entropy of  $x$  and the *conditional entropy* of  $y$  given  $x$ , i.e. the uncertainty of  $y$  when  $x$  is known. If meerkats never moved, the second call would be entirely redundant – its conditional entropy would be 0. If meerkats typically move within 10 seconds with a 50% probability, then another call 10 seconds later by the same individual from the same location conveys one bit of information etc. However, these back-of-the-envelope calculations depend on many assumptions about meerkat psychophysics, patterns of movement etc, for which ethologists do not have supporting evidence (see also Beecher, 1989) although they might be able to collect them. Some of those assumptions might be better investigated in the laboratory than the field, but the fact that they have not been investigated does not undermine the utility of talking about communicative information despite our present inability to assign an exact entropy value for the communication.

To say that meerkats obtain information about the location of individuals from their ‘close’ calls is not to say that these vocalisations have phonologically distinct elements for different locations. They are ‘articulated’ for location of utterance (in the sense of Millikan, 1984) only in the sense that their location is a significant aspect of the sign. Human language allows us to say things that articulate range and direction relative to another person by varying not just the location of utterance but also the form of the acoustic signal, such as “On your left!” versus “On your right!” Production of such statements is a cognitively complex task because successful allocentric references to the other person’s left or right require the signaller to predict how the receiver will interpret ‘left’ versus ‘right’, in some sense adopting the receiver’s point of view. Given the desire to communicate position rapidly, when the situation permits, people are much more likely to say “Here!” or “Hey!” and rely on the receiver’s ability to discriminate who said it and from where. In principle, any vocalisation whatever would do, even if its conventionalised meaning is unrelated (“I hear the gooseberries are doing well this year...”) or opposite (“I’m not here”) to the location and identity information extracted by the receiver. However, because they require superfluous processing, such fanciful examples would be inefficient as signals whose primary function is to maintain social cohesion smoothly. Alternatively, a sound that is lacking in conventional meaning but still conventionalised (“hey!”) is a quite effective tool for communicating

location to a receiver. The physics of vocalising supplies the information needed for individual identification and the physics of sound travel provides direction to the source, while the receiver takes care of decoding the message. Informational and physical aspects of signals co-exist.

This notion of information does not fit the conception of meaning provided by the standard message-passing conception of language. Recalling Marler's (1961) claim that the significance of signals to the communicants – what he calls 'pragmatics' – should be our focus, I argue that it is the right conception of information for the study of animal communication (and perhaps a good alternative to the message-passing model for human language, too, but there is no space to defend that here; cf. M. Ramscar, in preparation). Some aspects of animal communication are conventionalised, albeit not to the same degree that human language is. Insofar as there are social mechanisms within a group of communicators that serve to stabilise the communicative functions of specific signals, the significance of these calls will be partly conventionalised, although contexts will allow for a lot of variation in the information that receivers impute. Even the absence of such mechanisms – which are not involved in maintaining the relationship of vocal quality to identity unless imitators are dissuaded by social means – the influence of such signals on receivers is highly dependent on what information receivers already have.

So long as the meerkats' 'close' calls follow the normal, smooth pattern of meerkat movements and interactions, the influence that signallers have on receivers is rather subtle. But when a call is perceived from an unexpected location, the influence is much greater. The difference that otherwise identical calls have on an audience requires us to take account of the role of receivers in imputing significance to them. The meerkat who hears a call from a completely unexpected direction is surprised. In a psychological sense, its uncertainty appears to have increased as it looks in the direction of the second call as if searching for confirming evidence. But if the function of the call is to communicate location, and communication involves reduction of uncertainty, how is this possible? The meerkat's surprise seems unlikely to be explained simply in terms of the change in subjective probability attached to the other's location because the initial call produces a comparable change without engendering surprise. Nor does Shannon's measure allow negative entropy, i.e. increase of uncertainty. We should be mindful of possible mathematical alternatives to Shannon's account (see Vigo, 2011, for a mathematical account of categorical information that does allow negative information). Nevertheless, it is possible to make sense of the meerkat's psychological uncertainty as a case of *miscommunication* that provides information about the signaller and the code.

In Shannon's engineering context, there is an idealised communication system in which sender and receiver share a fixed code and the task of the ideal receiver is to use the signal to reconstruct the message encoded by the signaller, i.e. to select one message from a predetermined set of possible messages (Shannon, 1948, p. 5). Miscommunication in this kind of idealised system consists solely in the receiver's selecting the wrong message. However, in the real world of communication between cognitively complex agents, including meerkats, the code is not uniquely determined in advance. Each signal can be considered as potentially encoding not one message but a range of possible messages, serving multiple possible purposes. Successful communication systems are shaped by social and natural selection pressures that enable signallers and receivers to converge, more or less, on signals that serve their biological purposes. But such convergence generally happens not because one precise message comes to be associated with each signal. Rather, the process requires continuous adjustments of signallers' and receivers' expectations against the background of a dynamic set of experiences. The predominant role of individual experience in interpreting signals is, I believe, why Marler emphasised pragmatics ("the significance of signals to the communicants") over semantics (a fixed relationship of signs to meanings) in the study of animal communication. When a signal violates expectations, it could be because a low-probability event occurred, because the signal was misperceived or because the communication system itself is not what was assumed. In this way, violated expectations provide evidence of real-world miscommunication. Such violations may provide information about the larger system of signals and messages that receivers must learn about. The surprised meerkat may have received a signal that normally would reduce uncertainty about the present location of the signaller, and so we may talk about the content of the message in this relatively context-free way. But as an interpretant, the meerkat has received information about the whole system of communication in which it is embedded. This information is not, however, encoded in the signal it received, and thus we do not have to say that it was communicated. Nevertheless, the cognitive animal can use information about the unlikelihood of the message it imputed to learn something about the reliability of the signaller and of the communicative system itself, and thus it looks around to learn more.

### 13.5 Conclusions

Messages have meaning, according to Shannon, by which he meant that "they refer to or are correlated according to some system with certain physical or conceptual entities" (1948, p. 3). But, he explained, such meanings are not

relevant to the engineering problem of designing efficient communication channels. Shannon (1956) urged caution about extending the engineer's concept to biology and psychology, but he was also optimistic that the theory would prove useful. I believe that neither side of the recent dispute has fully absorbed Shannon's lessons.

The reference to information in animal communication is not bound to metaphors drawn from human language. The Marlerians are right that the information eliminativists attack a straw man, although I am sympathetic to some elements of their critique. More can and should be done to connect the mathematics of information to claims about animal communication, but mathematical modelling is not an absolute requirement for progress to be made. There are general benefits to mathematical models, namely more precise predictions, and Shannon's seminal theory is a natural starting point. But there may be other ways of building mathematical models of information that would be even more useful for cognitive science (Vigo, 2011). Nevertheless, it is worth re-emphasising that Shannon's theory has held centre stage for many solid reasons, and given its seminal status, the theory is a natural starting point.

There is information available from communicative signals. The communicative systems of animals do not have the full structure of human language (see also McAninch, Goodrich & Allen, 2009). Nonetheless, the signals are appropriately described in terms of meaning or significance. That significance derives from an objective relationship between signal and source, but requires an organism to interpret it. One and the same signal has different significance to different receivers, or to the same receiver at different times. Owren *et al.* claim that ethologists should be cautious about using the metaphors of 'transmission', 'container' and 'conduit' (Owren *et al.*, 2010, p. 760) because they prefer to focus on the ways in which signals influence the emotions and behaviours of perceivers rather than presupposing a message literally being conveyed from signaller to receiver. I also urge caution about these metaphors, but for a different reason: they tend to reinforce the idea of fixed messages being passed between communicants through well-defined channels. The system is a lot more malleable than that, and communicators have various strategies for adjusting to violations of their expectations. Understanding these adjustments requires attention to the epistemically significant learning capacities of animals – they are not just influenced, but they actively seek additional information when expectations are violated. Here, information models have strong leverage over mere influence models because they connect to learning theory in deep ways (M. Ramscar, in preparation).



The information eliminativists urge attention to affective-emotional processes in understanding animal communication rather than information processing, but following Marler, I believe this to be a false dichotomy (again, see McAninch *et al.*, 2009). Emotions are part of the information-processing system, not separate from it (Damasio, 1995). A meerkat that is surprised on hearing a ‘close’ call from an unexpected direction becomes aroused and alert, actively acquiring more information. Differential responses to repeated calls in the meerkats are not due to the intrinsically arousing properties of ‘close’ calls. The effect of a second call from the same individual within a few seconds and coming from the opposite direction is explained in terms of the informational state of the meerkat in relation to both calls. Contra Owren *et al.*, so long as we have to take into account the receiver’s informational state to make sense of its reaction to the signal then we cannot regard the meerkat as solely driven by a fixed relationship between physical properties of the signal and an emotional/affective response. Smooth communication fails when expectations are violated. But expectancies exist only in those organisms which impute significance to the signals they receive.

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