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Essay

The central importance of information in studies of animal communication

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The concept of information plays a central role in studies of animal communication. Animals' responses to the calls of different individuals, to food calls, alarm calls, and to signals that predict behaviour, all suggest that recipients acquire information from signals and that this information affects their response. Some scientists, however, want to replace the concept of information with one based on the 'manipulation' of recipients by signallers through the induction of nervous-system responses. Here we review both theory and data that argue against hypotheses based exclusively on manipulation or on a fixed, obligatory link between a signal's physical features and the responses it elicits. Results from dozens of studies indicate that calls with 'arousing' or 'aversive' features may also contain information that affects receivers' responses; that acoustically similar calls can elicit different responses; acoustically different calls can elicit similar responses; and 'eavesdropping' animals respond to the relationship instantiated by signal sequences. Animal signals encode a surprisingly rich amount of information. The content of this information can be studied scientifically.

The concept of information has played a long and productive role in the study of animal communication. Empirical research has attempted to specify the kinds and amount of information transferred in signalling systems as disparate as the dance language of honeybees (von Frisch 1967; Seeley 1997), the claw-waving displays of crustaceans (Dingle 1969), the songs of birds (Vehrencamp 2000), and the alarm calls of primates (Cheney & Seyfarth 1990). Theoretical analyses have relied heavily on the concept of information in contexts ranging from aggression to courtship to cooperation (Enquist 1985; Grafen 1990; Maynard Smith 1991).

Nevertheless, this approach has been criticized by a minority of researchers. Dawkins & Krebs (1978, page 309), for example, argued that animal signals should be viewed not in terms of information but in terms of the manipulation of receiver behaviour, arguing that 'it is probably better to abandon the concept of information transfer altogether'. The call to abandon information in favour of 'manipulation' or 'assessment/management' was later renewed by Owings & Morton (1997, 1998), who suggested that 'the informational perspective is not adequate as a concept or methodology to understand either the evolution or the process of vocal communication' (1998, page ix). Along with others, they advocate a view of communication as management by signallers of the behaviour of receivers (see also Owren & Rendall 1997, 2001; Owren 2000; Rendall et al. 2009). For example, following Morton (1977), Rendall et al. (2009) note that the squeaks, shrieks and screams of many animals have 'sharp onsets, dramatic frequency and amplitude fluctuations, and chaotic spectral structures, which are exactly the sorts of features that have direct impact on animals' nervous systems' (page 236). Similar generalizations hold for alarm calls which have evolved, they believe, to 'induce nervous-system responses' in receivers (Owren & Rendall 2001, page 61). Finally, the critics also argue that using terms like information implicitly commits scientists to the use of human communication, particularly language, as a model for communication in animals. It is therefore both anthropomorphic and inaccurate (Owings & Morton 1997, 1998).

These opposing views find parallels in studies of animal learning. For years, behaviourists argued that the mental activities of animals were not appropriate topics for research, either because they could not be studied scientifically (methodological behaviourism) or because they did not exist (radical behaviourism; Skinner 1974).

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Today, however, this view has largely been discarded. Modern theories of learning have a strong cognitive component, with many experiments designed to examine the content of animals' knowledge and the information that animals acquire as a result of experience (e.g. Colwell & Rescorla 1985; Kamil 1987; Rescorla 1988; Lieberman 2003).

CLARIFYING THE TERMINOLOGY

Current accounts of information are built on the theoretical advances made by Shannon (1948) and Wiener (1961). Shannon viewed information as a statistical measure of uncertainty, allowing for mathematical analyses of information processing. While information theory was initially developed to describe information transmission in technical systems, it quickly found its way into a range of other disciplines, including psychology and animal behaviour (e.g. Dingle 1969; Beecher 1989). For our purposes, treating information as a reduction of uncertainty in the recipient is useful because it connects communication to learning theory and to research on the mechanisms by which animals associate signals (or cues) with each other or with the outcomes of specific behaviours.

INFORMATION IN ANIMAL COMMUNICATION

Whenever there is a predictable relation between a particular signal and a specific social situation, the signal can be used by listeners to predict current states or upcoming events; that is, to provide information. A light that predicts shock, an alarm call that predicts the presence of an eagle, or a scream that predicts that a specific individual is involved in a fight all have the potential to provide a listener with information if they are reliably associated (Rescorla 1988) with a narrow range of events (Seyfarth & Cheney 2003). In each case we assume that the listener has acquired the contingent relation between two stimuli and thus reduced its uncertainty (or gained information) about events in the world: the light predicts shock, not food; the alarm call predicts an eagle, not a leopard; the screams predict that one individual, but not another, is involved in a dispute. We also assume that learning such associations (if learning is required) is adaptive because it allows the receiver to predict what is likely to happen next.

Empirical support for this use of information is widespread in studies of animal communication. It is now clear that individuals in many species consistently use specific signals in particular social or ecological contexts and that receivers have learned or otherwise acquired these contingent relations, gaining information as a result. For example, honeybees, *Apis mellifera*, acquire information about the location of food by observing the details of a worker bee's dance (e.g. Seeley 1997). In hermit crabs, *Pagurus bernhardus* (Laidre 2009), swamp sparrows, *Melospiza georgiana* (Ballentine et al. 2008), and banded wrens, *Pheugopedius pleurostictus* (Vehrencamp et al. 2007), certain visual or vocal displays are reliable predictors of an individual's subsequent aggressive behaviour, and recipients respond as if they know this relation. The begging calls of cliff swallows, *Hirundo pyrrhonota*, are individually distinctive and provide parents with information about individual identity; the begging calls of barn swallows, *H. rustica*, do not (Medvin et al. 1993). In black-capped chickadees, *Poecile atricapillus*, acoustic features of the 'seet' and 'chick-a-dee' alarm calls are correlated with both the type of predator present and the degree of danger. Playback experiments indicate that listeners acquire this information from the calls (Templeton et al. 2005). A similar generalization holds for the alarm calls of African suricates, *Suricata suricatta*. Suricates give acoustically different alarm calls to different predators (jackals, eagles and snakes), and within each call type produce calls with graded acoustic variation that is correlated with the urgency of the danger. The suricates' responses to call playbacks suggest that, upon hearing an alarm call, individuals acquire information about both predator type and urgency (Manser et al. 2001a, b). In California ground squirrels, *Spermophilus beecheyi*, acoustically different alarm calls encode information about urgency, but not predator type (Owings & Hennessy 1984); in primates, they encode information about different predators (vervet monkeys, *Chlorocebus aethiops*: Seyfarth et al. 1980; Diana monkeys, *Cercopithecus diana*: Zuberbühler et al. 1999). Macedonia & Evans (1993) discuss the evolution of alarm call systems that encode different types of information. Finally, in addition to their acoustically different alarm calls for ground and aerial predators (Evans et al. 1993), domestic chickens, *Gallus gallus domesticus*, produce food calls that signal the presence of food. Once again, playback experiments indicate that listeners acquire this information from the calls (Evans & Evans 1999, 2007).

Contrary to the critics' argument, investigators in these studies have not naïvely applied linguistic concepts to their subjects, nor have they claimed that their results demonstrate the same kind of information transfer found in language. Instead, they have simply tried to determine whether particular signals predict something about the world (e.g. the presence of food, the caller's identity, a particular kind of predator, or the urgency of danger) or about the signaller's next behaviour. In this respect, the critics have set up a straw man: although information plays a central role in studies of animal communication, ethology is in no danger of being taken over by linguistics.

The 'manipulative' approach also leaves many interesting questions unanswered. For example, some of the alarm calls mentioned above have acoustic features that are arousing and attention getting. Why, then, are the calls within each species acoustically so different? Why do individuals respond to them in such different ways? And why is there such wide variation across species in the acoustic properties of alarm calls? Rats' alarms have a whistle-like structure (Litvin et al. 2007), those of shifaks are low-frequency roar grunts (Fichtel & Kappeler 2002), while antelope produce snorts (Tilson & Norton 1981). An exclusive focus on the calls' arousing physical characteristics cannot answer these questions.

Nor does the presence of particular acoustic features preclude the acquisition of information by listeners. Primate screams, for example, may have 'aversive' acoustic qualities, but this does not preclude recipients from acquiring information from them. In fact, research on many primates has shown that screams are individually distinctive (e.g. Hammerschmidt & Fischer 1998). Their acoustic features can also be correlated with different types of aggression (Gouzoules et al. 1984), the caller's role in the interaction (Slocombe & Zuberbühler 2005), or the presence of a particular 'audience' (Slocombe & Zuberbühler 2007). As a result, screams used in playback experiments elicit different responses from different individuals, or from the same individual under different circumstances (Cheney & Seyfarth 1980; Gouzoules et al. 1984; Palombit et al. 1997; Fischer 2004; Fugate et al. 2008; Slocombe et al. 2009). Here again, an exclusive focus on the screams' aversive qualities cannot explain these results.

Theoretical Limitations

The critics argue that signals have evolved to manipulate listeners' behaviour, and that the acoustic properties of signals take the form that they do because they have a 'direct effect' on listeners' nervous systems, effects that are difficult for listeners to resist. This explanation assumes that listeners are automata that can be manipulated to respond in ways beneficial to the signaller as long as the right nervous-system buttons are pushed. However, as Searcy & Nowicki (2005, page 8) point out, 'The critical flaw with