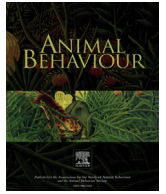




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The origin of meaning in animal signals

Robert M. Seyfarth^{a,*}, Dorothy L. Cheney^b^a Department of Psychology, University of Pennsylvania, Philadelphia, PA, U.S.A.^b Department of Biology, University of Pennsylvania, Philadelphia, PA, U.S.A.

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Over 40 years ago, Peter Marler proposed that animal signals were adaptive because they provided listeners with information (Marler, 1961, *Journal of Theoretical Biology*, 1, 295–317). But what was the nature of this information? How did it influence behaviour? And how might the information in animal signals compare with the information in human language? Here we review evidence that signals in a variety of social contexts are adaptive because they convey information. For recipients, meaning results from the integration of information from the signal and the social context. As a result, communication in animals – particularly in long-lived, social species where the same individuals interact repeatedly – constitutes a rich system of pragmatic inference in which the meaning of a communicative event depends on perception, memory and social knowledge. In the human lineage, pragmatics served as a precursor to the later evolution of semantics and syntax. Among primates, there is a striking difference in flexibility between constrained call production and more flexible perception and cognition. However, call production is more flexible in the wild, where it is affected by contextual cues, than in laboratory studies where contextual cues have been removed. Monkeys and apes may overcome the limits of constrained vocal production by producing composite signals in the same and different modalities.

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In this essay we focus on an issue that was central to Peter Marler's research on animal communication: the meaning of animal signals.

Research on animal communication has made almost no progress in understanding the semantics of natural signaling behavior because it is an exceedingly difficult problem in both practical and theoretical terms. ... There is an irresistible tendency to use language as a model, either for comparison or contrast. This would be more appropriate if we really understood human semantics and the processes by which language acquires meaning in the course of our own early development. In many respects our picture of how words acquire meaning in human infancy is hardly any clearer than our understanding of the meanings of signals for animals ... In both human and animal studies, for example, there are assertions of the overwhelming importance of contextual cues in understanding meaning (Smith, 1977), but precisely how the context influences meaning in particular cases has hardly been explored.

(Marler, 1983)

Marler's interests in the meaning of animal signals brought him squarely into the revolution in neurobiology, psychology, linguistics and cognitive science. When he began his research in the 1950s, questions about the 'minds' of animals had largely been ignored, because both psychologists like Skinner and ethologists like Tinbergen thought they were unanswerable and hence unsuited to scientific inquiry (Boakes, 1984; Burkhardt, 2005). Over the years, Marler developed a different view (Marler, 1961). He thought that, regardless of whether or not they were voluntary or intentional, animal signals provided listeners with information. But what was the nature of this information? Was it stored in memory so that it could affect future interactions? And particularly in monkeys and apes, could we find evidence for something like the 'mental representations' that were currently coming to light in human psychology, linguistics and cognitive science?

Here we review progress that has been made in answering these questions in the years since Marler first drew attention to them. We begin with evolution. Communication has been shaped by natural selection. Signallers would not produce signals if doing so were not beneficial to them, and receivers would not respond if doing so were not beneficial to them. But the signaller and the recipient are sometimes competitors, sometimes cooperators, and often a bit of both. How does communication achieve these two, sometimes

* Correspondence: R. M. Seyfarth, Department of Psychology, University of Pennsylvania, 425 S. University Avenue, Philadelphia, PA 19104, U.S.A.

E-mail address: seyfarth@psych.upenn.edu (R. M. Seyfarth).

contradictory, benefits? Studies of baboons and macaques, together with theoretical models, demonstrate how cheap signals that convey reliable information can become evolutionarily stable in social groups where competition and cooperation are inextricably entwined.

Next, we consider the link between communication and cognition. Following Marler and many others, we argue that most communicative events are adaptive for both signaller and recipient because signals reduce the uncertainty inherent in any social interaction. They do so by providing information. Where does it come from? We argue that, whereas some signals by themselves can provide recipients with specific information, many signals are vague. Signals do not occur in a vacuum, however. They are, instead, embedded in a rich social context where animals know each other and have a long history of interaction. This contextual information frames each communicative event, enormously enriching what a signal means. Borrowing a term from linguistics, we propose that animal communication constitutes a rich pragmatic system. The ubiquity of pragmatics, combined with the relative scarcity of semantics and syntax, suggest that as language evolved semantics and syntax were built upon a foundation of sophisticated pragmatic inference (Seyfarth & Cheney, 2014a, *in press*).

Finally, as Marler (1965) first noted, vocal production in nonhuman primates – and indeed most mammals – is highly constrained. How, he wondered, could such a limited system of production function in such a richly varied, ever-changing social environment? Subsequent research has shown, as Marler first predicted, that call production is not as rigid and reflexive as originally believed: contextual cues can affect call type, call acoustics, and whether an animal calls or remains silent. Marler also suggested that nonhuman primates overcome the constraints imposed by a limited vocal repertoire both by combining calls with visual signals and by combining different call types with each other ('composite' signals: Marler, 1965). Here again, his suggestions have proved prescient: we discuss some recent examples.

THE EVOLUTION OF SOCIAL SIGNALS

Animals are often involved in overtly competitive interactions: over food, territory, or mates. But rather than immediately escalating to physical fighting, competition is more likely to take the form of displays, like the roars of red deer, *Cervus elaphus* (Clutton-Brock & Albon, 1979), the jousting of stalk-eyed flies (Wilkinson & Reillo, 1994), the croaking of male frogs (Ryan, 1985), or the loud wahoo calls of male baboons (Fischer, Kitchen, Seyfarth, & Cheney, 2004; Kitchen, Seyfarth, Fischer, & Cheney, 2003). Thanks to decades of empirical research (reviewed in Bradbury & Vehrencamp, 2011; Searcy & Nowicki, 2005) and pioneering theoretical work (Enquist, 1985; Grafen, 1990; Maynard Smith, 1991; Zahavi, 1975), we now have an explanation of why these displays are evolutionarily stable. To cite just one example, in red deer the fundamental frequency (F0) – or, more accurately, formant spacing – in a male's roar is constrained by his body size, which in turn predicts his competitive ability (Reby et al., 2005). Formant spacing is an honest, unfakeable cue because small males cannot make deep-pitched roars. And because formant spacing accurately predicts competitive ability, selection has favoured listeners who decide to escalate or retreat based in part on this acoustic cue. From the listener's perspective, honest signals provide a reliable way to assess an opponent quickly and with minimal risk (Searcy & Nowicki, 2005). If the listener cannot make an assessment (because, for example, roars are so alike that they cannot be distinguished), the interaction escalates to include additional signals or behaviour that reduce the participants' uncertainty, like the 'parallel walk' in red

deer (Alvarez, 1993; Clutton-Brock & Albon, 1979; see Searcy & Nowicki, 2005, for further discussion).

But what about the many other signals that animals use in less competitive, more cooperative circumstances? Can the same argument be applied? Consider, for example, the grunts given by female baboons (*Papio cynocephalus ursinus*) as they approach mothers with young infants. Like all female primates, female baboons are highly attracted to infants; however, mothers are often reluctant to allow access to their infants, particularly when the approaching individual is of higher dominance rank (Silk, Rendall, Cheney, & Seyfarth, 2003). Mothers rarely initiate interactions with prospective handlers, and when other females approach them, mothers' reactions range from passive acceptance to overt avoidance (Silk et al., 2003). For all of these reasons, the individuals involved in this communicative event are, in a mild way, competitors.

At the same time, infant handling is common among females and occurs even when the two females are highly disparate in rank. It is often accompanied by grooming and occurs at high rates among individuals that may live for many years together in groups where repeated interactions are common and long-term social bonds with consistent partners are positively correlated with reproductive success (Silk et al., 2009, 2010a, 2010b). For all of these reasons, the individuals involved are not exactly competitors – in many respects their interests overlap.

Grunts facilitate infant handling. When a female gives a series of grunts as she approaches a mother with infant, the mother is significantly less likely to move away than if the approaching female remains silent (Cheney, Seyfarth, & Silk, 1995). How do grunts achieve this outcome? In a study of rhesus macaques, *Macaca mulatta*, where females' interest in infants is also high and grunt and girney vocalizations facilitate infant handling, Silk, Kaldor, and Boyd (2000) found that grunts and girneys accurately predicted the approaching female's subsequent behaviour: if she grunted, aggression was significantly less likely and grooming was significantly more likely than if she did not. In other words, there was a contingent, predictable relation between the approaching female's vocalizations and what she did next. Mothers had come to recognize this contingency and treated grunts and girneys as honest indicators of the approaching female's benign disposition. Just as in any learning experiment – or any competitive interaction – mothers acquired information from signals. This information reduced their uncertainty and affected their behaviour.

Following Maynard Smith (1991, 1994), Silk et al. (2000) developed a model demonstrating that honest, low-cost signalling can be an evolutionarily stable strategy (ESS) even when there is conflict of interest between the individuals involved, as long as the individuals interact repeatedly. Such signalling is particularly likely to evolve when individuals rank the value of possible outcomes in the same order (for example, by preferring a friendly outcome over an aggressive one) or evaluate outcomes differently but place some value on coordination. This result is important because it suggests that honest, low-cost signalling can evolve under a wide variety of conditions. Indeed, the conditions that are most favourable to its evolution are those commonly found in groups of social mammals.

INFORMATION

Evolutionary models of communication invoke the concept of information, but their exclusive focus on function leaves them agnostic about the content of information or how it is acquired. Grafen (1990, page 521), for example, stated that 'at ESS the receivers will have adjusted their assessment rule so that they determine correctly the true quality of a male', but he did not

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