

The evolution of functionally referential meaning in a structured world

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Abstract

Animal communication systems serve to transfer both motivational information—about the intentions or emotional state of the signaler—and referential information—about external objects. Although most animal calls seem to deal primarily with motivational information, those with a substantial referential component are particularly interesting because they invite comparison with words in human language. We present a game-theoretic model of the evolution of communication in a “structured world”, where some situations may be more similar to one another than others, and therefore require similar responses. We find that breaking the symmetry in this way creates the possibility for a diverse array of evolutionarily stable communication systems. When the number of signals is limited, as in alarm calling, the system tends to evolve to group together situations which require similar responses. We use this observation to make some predictions about the situations in which primarily motivational or referential communication systems will evolve.

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1. Introduction

Most of the signals that animals use to communicate with one another do not seem to have a specific meaning in the same sense that nouns in human language do. Rather, these signals communicate about the intentions, emotional state, or identity of the sender. For example, the song of a male Darwin's finch is thought to identify him as such to conspecific females (Grant and Grant, 1997). Little blue penguins use calls to signal their readiness to escalate a fight (Waas, 1991). Even the alarm calls given by ground squirrels, which were once thought to indicate the type of predator, have been shown instead to relate to the degree of urgency perceived by the caller (Robinson, 1981). However, there are other animal communication systems in which the signals really do seem to refer to some external stimulus. Most famously, vervet monkeys use three qualitatively different alarm calls to distinguish between leopards, eagles and snakes (Cheney and Seyfarth, 1990). Similar predator-specific calls have been found in other

primate species (Macedonia, 1990; Zuberbühler et al., 1997) as well as suricates (Manser, 2001) and chickens (Evans et al., 1993). This type of system is not limited to predator warnings alone: toque macaques (Dittus, 1984) and chickens (Evans and Evans, 1999) produce specific calls which alert others to the presence of food.

Semantic communication has been suggested as one of the fundamental differences between animals and humans (e.g. Bickerton, 1990). The communication systems described above, though relatively rare, are of special significance because they hint at the ability of animals to communicate about external objects and events. But does a leopard alarm call really refer to a leopard, in the same sense that the word “leopard” does? Philosophers of language contend that understanding how an utterance is used is insufficient to determine its meaning (Grice, 1957; Quine, 1960); according to this view we can never discover the true meaning of any animal signal. Ethologists have instead focused on demonstrating that some animal signals have the property of *functional reference*: the way in which they are used, and the responses that they engender, give the appearance of referring to some external stimulus (Marler et al., 1992; Macedonia and Evans, 1993). The

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notion that animal signals may have some external referent is not diametrically opposed to the idea that they convey motivational information; rather, it is now well recognized that, like human language, animal signals may simultaneously do both. Still, it is possible to differentiate between systems like the vervet monkeys', which primarily refer to external objects, and systems like the prairie dogs', which primarily reflect the degree of urgency; we are interested in the evolutionary reasons behind this kind of difference.

In this report, we present a model for the evolution of functionally referential meaning in animal communication systems. We begin with a simple action–response model in which selective pressure on the production of the signal is produced by the reactions of those who respond to it, and vice versa. Selection on signals and selection on responses will often work towards one another, eventually leading to a stable and coherent communication system, as has been demonstrated previously with similar models (Hurford, 1989; Wärneryd, 1993; Nowak and Krakauer, 1999). However, these models invariably assume that the world itself takes on a very simple structure: each situation requires a particular, unique response, and all possible alternatives are equally inappropriate. Although this may be an adequate representation of certain economic games, it does not describe animal signalling interactions very well. For example, when a vervet monkey is approached by a leopard, the typical response to an eagle—looking up and running into cover—is much more dangerous than the typical response to a snake—scanning the area (Seyfarth et al., 1980).

In our model of communication in a “structured world”, we are able to represent the distinction between not-quite-optimal actions and utterly disastrous ones. We find that a wider variety of signalling systems are evolutionarily stable in our model than in the unstructured worlds of previous models, and this diversity of equilibria more accurately reflects the diversity of modern animal communication. In addition, our model suggests that evolved communication systems may facilitate the categorization of events or situations by appropriate responses, rather than by shared physical characteristics. This may explain why primarily motivational alarm call systems, like that of ground squirrels, are so common, while primarily referential ones, like the vervets', are relatively rare. If motivational states (like fear, arousal, or hunger) have evolved to help organisms make advantageous decisions, then in many cases they may be sufficient to predict an appropriate response to the situation, and thus sufficient to determine which signal to produce. Only in special cases, where the possible reactions are too complex to be determined simply by the urgency of the situation, will a system evolve the characteristic of functional reference.

2. A model for the evolution of communication

Since we are interested in modeling the way that a signal, through use, may come to represent an object or a situation, we begin with a simple sender–receiver game.

One individual responds to a stimulus in some observable way; another individual observes that response and reacts in turn. The first individual's action has no power to affect her payoff, while the second individual's reaction affects the payoff of both. In this sense, the first individual's action may be seen as a potential signal to the second individual; it is only through natural selection that these actions gain the status of true signals, as defined by Maynard Smith and Harper (2003, p. 3): “an act or structure which alters the behavior of other organisms, which evolved because of that effect, and which is effective because the receiver's response has also evolved.” Once natural selection begins to shape the behavior of individuals in both roles, all of the potential signals that are in use become real signals. Some of these signals may later fall out of use, preventing selection on the response. However, as long as some tendency to respond remains—however it may change through drift—they retain their power to be used as signals.

Now we can define the game more rigorously. The first player, the *signaller*, observes the state of the world $t \in \mathcal{T} = \{t_1, t_2, \dots, t_l\}$, and selects a signal $s \in \mathcal{S} = \{s_1, s_2, \dots, s_m\}$. The second player, the *signal receiver*, does not know the state of the world directly, but instead observes the signal s and chooses an action $a \in \mathcal{A} = \{a_1, a_2, \dots, a_n\}$. Note that the number of distinct signals, m , may be different from the number of states, l , or the number of possible actions, n ; we discuss the biological factors affecting the relative numbers of each at the end of this section. We will (conventionally, if somewhat unrealistically (Lachmann et al., 2001)) assume a purely cooperative game: both signaller and receiver obtain the same payoff $\pi(t, a)$, which depends only on the state of the world and the selected response. Since the payoffs are independent of the signal used, all signals are in this sense equivalent to one another. For simplicity, we also assume that all signals are transmitted without error.

In this sender–receiver game, the signaller's strategy can be represented by a matrix \mathbf{P} which contains the conditional probabilities $p(s|t)$ of producing each signal s , given each world state t . Similarly, the receiver's strategy is represented as a matrix \mathbf{Q} that provides the conditional probabilities $q(a|s)$ of selecting an action a , given signal s . Each individual can play both signalling and receiving roles, so a complete strategy R consists of both a \mathbf{P} matrix and a \mathbf{Q} matrix.

We can calculate expected payoffs, given a probability distribution on world states $p(t)$. If we further assume that each individual spends half the time as signaller and half the time as receiver, the expected payoff to an individual with strategy $R = (\mathbf{P}, \mathbf{Q})$ of interacting with an individual with strategy $R' = (\mathbf{P}', \mathbf{Q}')$ will be

$$\begin{aligned} \bar{\pi}(R, R') = & \frac{1}{2} \sum_{t \in \mathcal{T}} \sum_{s \in \mathcal{S}} \sum_{a \in \mathcal{A}} p(t) p(s|t) q'(a|s) \pi(t, a) \\ & + \frac{1}{2} \sum_{t \in \mathcal{T}} \sum_{s \in \mathcal{S}} \sum_{a \in \mathcal{A}} p(t) p'(s|t) q(a|s) \pi(t, a). \end{aligned}$$

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