Chapter 7

ANIMAL COMMUNICATION VIA COORDINATED COGNITIVE SYSTEMS

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I. ABSTRACT

To the extent that learning and memory play a role in communication in a given species, cognitive models of those processes can be useful for investigating the constraints on signal variability in that species. Such models are based on predictive regularities between sensory input and behavioral output and assume that the animal constructs and continually updates a mental representation of its world. In this approach, an animal's interactions are seen as being guided by a "cognitive system" consisting of innate perceptual and motor constraints as well as learned event correlations and contingencies for response. Such cognitive systems generate predictions about the behavior of others and enable the animal to adaptively modify its own behavior. In this context, communication is defined as the set of processes by which one cognitive system influences the output of another.

In order for communication to be effective, cognitive systems must be coordinated. That is, regardless of whether the interacting animals have communal or conflicting interests, they are under equal evolutionary pressure to engage in a coherent, mutually interpretable exchange. While species-specific constraints and social rituals promote shared expectations, some cognitive coordination must be negotiated. In this view, signals are produced not only to elicit a desired behavioral response but to assess and establish the cognitive preconditions for a range of potentially relevant responses. Thus, communicative efforts

may be adaptive if they facilitate similarities or undetected, strategic discrepancies (as in deception) between the participants' models of the world. As a result, communication is shaped by what animals know and need to know, by their current characterization of the context, and by their ability to represent how various critical relations between signals correlate with behavior.

II. VARIABILITY AND THE ROLE OF INTERPRETATION

Any discriminable behavior can communicate. Eating. Preening. Acting relaxed or tense. Even silence can send a loud and clear message. And, although many concerned with the nature and origin of animal communication have acknowledged this (e.g., Hinde, 1970; Bateson, 1972; Smith, 1977), such unconstrained diversity would seem to confound systematic analysis. As a consequence, much of the effort in this field—both theoretical and empirical—has been focused on discrete, often ritualized behaviors. The relatively invariant properties of such behaviors make them easy to observe and tabulate, and their more or less predictable use helps us to identify the conditions that elicit them. Plus, since it is the signal properties of such behaviors that presumably renders them adaptive, a study of their deployment and impact can reveal principles underlying the evolution of communication. But such an emphasis on evolved signals may divert us from factors necessary to a full account of the wide variety of behaviors that succeed in mediating animal interactions.

Some researchers have recently chosen to focus on the nature of the responses elicited by communication signals (e.g., Dawkins and Krebs, 1978; Hinde, 1981; Krebs and Dawkins, 1984). Such an interactive view is not altogether new; the coevolution of signalers has long been recognized by researchers in this field (e.g., Tinbergen, 1952; Lorenz, 1952). Ethologists have often pointed out, for example, the "selective tuning" (Smith, 1977) of an animal's vocal output to the auditory range of its target, as in the mating calls of cricket frogs (Capranica et al., 1973) and the subsonic rumblings of separated elephants (Langbauer et al.,1991). In fact, all species-specific signals, including songs, scents, or colorful markings, are adaptive precisely by virtue of their being detected and differentially responded to by conspecifics. Signal evolution is also influenced by the discriminative abilities of interspecific audiences, as evidenced, for example, by the difficulty predators have in localizing alarm calls. But even an emphasis on the coevolution of communication has tended to focus on relatively fixed, stereotyped behavior, again bypassing the issue of variability.

Nevertheless, an evolutionary account of communication does not have to preclude an analysis of variation. Such an account requires only that we realize

that among the mechanisms that produce both signals and responses are interpretive processes that have likewise been subject to natural selection. These interpretive processes have as their physical substrate a level of neurological development peculiar to vertebrates, which can become quite complex in birds and mammals. Such processes mediate between sensory input and behavioral output and determine the relevance and impact of stimuli. In contemporary comparative psychology, such processes are labeled "cognitive."

It is worth noting here that not all neurally mediated communication should be considered cognitive. Signals that are direct products of the habituation or sensitization of neurons, for example, along with certain maturation processes, would probably best be described in terms of their underlying physiology. However, once the processes of *learning and memory* come into play, the usefulness of cognitive models shifts radically. With only slight increases in neural complexity, our capacity to describe how neural mechanisms mediate behavior rapidly breaks down. Certainly at the level of birds and mammals, where the most variability in communication occurs, cognitive models are currently more proficient than neurological ones for describing these processes. Even artificial intelligence models, many of which are designed to mimic neural networks, and have had encouraging success in producing systems that "learn" (Rumelhart and McClelland, 1986), are not yet as fully developed as the models of comparative cognition. Thus, to the extent that learning and memory play a role in the production and interpretation of communication, cognitive models will be appropriate in discussions of this communication.

III. CONTEMPORARY MODELS OF ANIMAL COGNITION

Because the word "cognitive," to those outside the field of comparative cognition, tends to connote the complex reasoning processes in which humans engage, a few clarifying remarks may be in order. First of all, I am making no commitment here regarding the notion of "conscious" thought in animal communication (see Griffin, 1976; Ristau, 1990). I do not consider it necessary to establish whether or not animals "intend" to communicate, or "deliberately" choose a response, in order to profitably describe the cognitive mechanisms underlying such behavior. This is not to say, however, that an animal's mind must therefore be considered the "black box" of the Skinnerian behaviorists. The emerging discipline of comparative cognition is built on the supposition that something *can* be said about the nature of mental representations and the course of learning and decision making in many nonhuman animals (e.g., Mackintosh, 1974; Dickinson, 1980; Roitblat *et al.*, 1984). Regularities in input/output rela-

tions reveal constraints on the systems that produce them, and these constraints can be modeled as particular kind of mental events.

For example, consider the long-standing behaviorist conundrum of "behaviorally silent learning" (Dickinson, 1980; see also Tolman, 1948). Suppose an animal is, at first, merely exposed to repeated pairings of a light and a tone. Learning, traditionally defined as the change in the probability of behavior due to reinforcement contingencies, could not be said to occur in this context, since neither behavioral change nor reinforcement occurs. Suppose the animal is next reinforced for making a particular response in the presence of the light alone. While this change in behavior does not meet the traditional criteria, there is no accounting, in that framework, for the fact that, without additional training, the unreinforced tone also elicits the response.

In contemporary comparative models, learning is defined as the formation of mental representations of event correlations (e.g., Dickinson, 1980). Such a representation would be said to form, for instance, during the initial pairing of the light and tone. When the tone is later presented alone during testing, it elicits a representation of the light in the animal's mind and it is in expectation of the reward that has been associated with that light that the animal responds. The modern theories are still essentially behaviorist, however, in that they maintain that the only viable data are observable behaviors. What has changed is the set of inferences based on those data that are considered justifiable. Most contemporary researchers have found that postulating the mental representation of event correlations results in a more parsimonious model of animal learning, with greater explanatory power than the stimulus–response rules that once governed the mysterious black box. This axiom shift has engendered productive and unanticipated research on the nature of animals' representations and how they interact and change.

In this chapter, a cognitive system will be defined as the set constraints that influence the nature of the representations that an animal forms through learning. The representations so formed comprise associative correlations between experienced stimuli, the contextual salience, both inborn and learned, of certain dimensions (such as smells, of whatever type, being important in foraging), and response strategies that the animal has learned are more or less effective in various contexts. We will say that an animal forms a cognitive model of a particular situation when certain representations are especially available to the animal in that context, preparing it with expectations of upcoming events. These expectations may prompt the animal to action or may prime it to learn relevant, new information. Within this framework, we will define communication as the set of processes by which one cognitive system influences the output of another. Adopting this set of definitions, let us review the issues and research on animal communication and discover what insights may emerge from this contemporary perspective.

IV. RELEVANCE AND COGNITIVE ENVIRONMENTS

Some behaviors—digging a burrow, building a nest, biting an adversary, mating—directly affect an animal's physical environment. In the domain of communication, however, an animal's behavior often produces only incidental physical effects. Its primary impact is on the cognitive systems of another organism. It is this impact—in part a function of the receiver's own design constraints, previous experience, and current surroundings—that determines that organism's response. Thus, we might say that it is the cognitive environment, rather than the physical environment, upon which communicative behavior most directly operates. In this way, research in comparative cognition can be of value to the study of animal communication, since it offers a description of some of the important parameters of that cognitive environment.

Probably the most salient feature of a cognitive environment is that it does not replicate (in whatever code) the physical environment in which it operates. Each cognitive environment represents only a select subset of the information potentially available to it. Perceptual and attentional processes place one set of limitations on the sorts of stimuli that can be represented (for discussion, see Evans and Norris, 1988). Constraints on modality relations can also exert an influence, as in rats that will learn to associate olfactory but not visual cues with a subsequent illness (Garcia and Koelling, 1966). Such constraints are illustrative of a broader principle of "relevance" that seems to characterize the organization of all cognitive environments (see Sperber and Wilson, 1987). As we shall see, relevance is a key element in the intimate relationship between communication and cognition.

A relevant response can sometimes be more or less assured by innate perceptual/motor programs. Reflexes, such as sucking by infant mammals or jerking away from a burning touch, are obvious examples. Similarly, imprinting involves an inborn readiness to respond to pertinent stimuli at a particular stage of development. Even in predator/prey relationships, specialized circuitry exists to promote relevant responses. Certain moths, for example, can hear only the frequencies produced by moth-eating echolocating bats (Roeder, 1967). As a direct result of such stimulation at close range, these moths lose the ability to coordinate their wingbeats and thus move in an erratic, and presumably difficult to pursue, path. Just as we can learn about the nature of communication by examining such relatively "hard-wired" systems, so too can it be heuristic to study the patterns of organization in the cognitive environments that animals construct themselves.

Generally speaking, "relevance" translates as "biological importance," in terms of serving survival and reproductive imperatives. In practice, however, complex systems can require a vast array of subtle discriminations and assess-

ments to deal with the myriad subgoals generated in everyday life. The complex organism must, within its species' biological constraints, construct its own cognitive environment based on its experience of the world. It is within the context of this construction that stimuli, including signals, are interpreted.

The criteria for relevance in such systems tend to be less stimulus-specific than in those where the appropriate cognitive environment is, for the most part, "provided" by evolution. That is, what will tend to be effective in terms of promoting adaptive behavior will be more context-dependent than in simpler organisms. This context is actually a function of the interaction between the multifaceted input from the physical and social settings, and the current configuration of associations and response strategies in the animal's cognitive environment. The animal's learning history and the constraints on the types of predictions it can form influence just which aspects of its rich perceptual environment it will interpret as relevant. As we shall see, the cognitive environment so constructed will have a significant impact on what organisms can accomplish through communication.

V. PRAGMATICS

In the study of human language, the area concerned with what gets accomplished by communicative acts is called "pragmatics." Although clearly interrelated, pragmatics can be distinguished from syntax and semantics in that the latter focuses on signal structure and content while the former is concerned with why—to what end—signals are produced. Ethologists have long recognized the relevance of pragmatics for the study of animal communication (e.g., Marler, 1961; Smith, 1977; Snowdon, 1982; Dawkins and Krebs, 1978). Since it is often assumed that signaling is adaptive only when it provokes behavior with an outcome favorable to the signaler (or to its kin), it makes sense to study not just the nature of the signals themselves but their capacity for effect as well. To do this, researchers have tended to investigate how well particular signals predict particular outcomes (e.g., Caryl, 1979; Hinde, 1981). But since, in the current discussion, we are concerned with the effects signals have on cognitive systems—and only indirectly on behavior—we need a slant on pragmatics that also emphasizes its cognitive aspects. Such a slant has been provided by Sperber and Wilson (1986) in their book *Relevance: Communication and Cognition*.

In their development of the work of language philosopher H. P. Grice (1957, 1969, 1975), Sperber and Wilson are concerned with how *human* communication fosters and exploits "shared" cognitive environments. This sharing is based, they say, on an assumption of relevance. When one person says something to another, the listener interprets that utterance based on the assumption

that the speaker intended it to be relevant. That is, both speaker and listener are held to recognize that they share certain knowledge and assumptions—as a result of their similar cultural backgrounds, their previous experience with one another, and/or their immediate environment. The listener is to interpret what he hears as having been intended to make sense within that shared framework. Thus, for example, a wife may say to her husband "The kitchen window is stuck" in order to elicit his help in opening the window. He understands that she is asking for help by virtue of his assumption that, rather than simply stating a fact out of the blue, she intends that he realize that such a statement is most relevant in a context in which she wants the window open and in which they both know that he is liable to be able to open it. Although both Grice, and Sperber and Wilson, emphasize the role of intention in this model, I would argue that the basic principle of relevance that they discuss can be applied—sans intentionality—to all animal communication.

Although Sperber and Wilson do not explicitly present an evolutionary argument, they do suggest that human communicators do not usually have to work at recognizing relevance or at fashioning signals that will be seen as relevant. The relevance constraint, they say, is "built in" to the way minds are organized and languages are designed. Stimuli are recognized as "relevant," they say, to the extent that (1) they require minimal processing effort because of their high availability in context, and (2) their impact on the cognitive environment, in terms of strengthening or challenging established expectations, is large. I would similarly suggest that this constraint—although specialized for human communication—is characteristic of the evolution of communication in all species, although mechanisms surely vary.

Among the expectations that constitute a human's cognitive environment are assumptions about the intentions, beliefs, and other mental states of others. We construct such assumptions by applying generally reliable heuristics regarding, for example, co-presence and thus co-access to available information, prior experience with others, the conventions of community membership, etc. (Clark and Marshall, 1981; see also Levinson, 1990). Since all members of a culture or subculture are liable to rely on similar mechanisms, the chances of individuals sharing what Sperber and Wilson call "mutual cognitive environments" are fairly good—at least good enough to support or at least initiate many conversations.

But ANY mechanisms that could reliably produce a "mutual cognitive environment" in communicating individuals would assure the relevance of signals. That is, assumptions about the mental states of others are not necessary for coordinating cognitive environments as long as some mechanism is reasonably likely to produce such coordination. In addition, within such a system, an animal would not need to recognize or intend to initiate the interpretation process; it must only do what works. But animal signals do work because the cognitive systems that produce and interpret them are designed by evolution to be coordi-

nated. In fact, a game theoretical analysis of communication suggests that this is necessarily the case.

VI. SIMILARITY AND STRATEGIC DISCREPANCY

Oftentimes, in both human and nonhuman communication, coordination entails developing a *similarity* of cognitive environments. Such similarity can be facilitated by physiological mechanisms, such as shared perceptual abilities. These shared abilities, as one type of cognitive constraint, lead to similarity in the detection and representation of species-important events. Social factors are also often important. Group coherence, for example, tends to expose all members to similar stimuli, including one another. Likewise, dominance hierarchies or other organizational structures establish roles marked by characteristic behaviors that are presumably similarly represented by all group members. Such mechanisms enable conspecifics to "assume" that they share cognitive environments—or, to be more precise, to act as if this assumption is justified. Species-specific signals are thus often readily recognized as relevant.

Sometimes however, animals must negotiate the coordination of their cognitive models. If, for example, two animals have similar representations of their relative rank in a social group, a signal by one will tend to elicit a predictable response from the other. If, on the other hand, their representations on this score differ, their "conversation" may need to be prolonged until one brings the representation of the other more into alignment with its own. Each animal brings a model to bear that anticipates certain behaviors that it has observed in similar situations in the past. If these expectations are not met, the animal is alerted by the discrepancy.

One response to such a discrepancy is for the animal to engage in other behaviors consistent with its own model. This is most likely if the animal is highly motivated, as by potential access to a valuable resource, and if, in its experience, the inconsistent behavior of its opponent is of a sort susceptible to change. Alternately, it may respond to the unexpected event by altering its model. That is, it may learn something new about the relationship and thus change its representation of the pertinent correlations. Its new model may now be more similar to that of its opponent. When both animals' behavior accords with the predictions of a mutual model, their relationship, at least for the moment, will be stabilized. Thus, the behaviors they display during such an encounter communicate, by our definition, in that they serve to coordinate the animals' cognitive systems.

Coordination does not necessarily entail cognitive similarity, however. Cognitive environments with very different representations can still be coordinated,

as long as a signal generated by one is interpreted by the other in such a way that mutually predicted behavior is ultimately produced. This is coordination in the game-theoretical sense, where the success of one system depends on a particular organization of the other. Interspecies communication, for instance, almost certainly involves the coordination of quite different cognitive environments. Even within a species, communication may involve one animal altering the cognitive environment of another in such a way as to set up a strategic difference between them. If only one particular kind of difference will successfully elicit the desired behavior, then arranging just that discrepancy is again an act of coordination.

An example of strategic discrepancy arises in deception. Among humans, Grice and others (see Mitchell and Thompson, 1986) have pointed out that in order for a lie to succeed, the listener is required to assume that the speaker is playing by the rules (i.e., Grice's "maxims of communication") and telling the truth. Thus, the speaker must skillfully fashion his lie to fit what he thinks his listener will accept as truth. To do this, he will draw on his past experience with her, or with other such listeners, and make a remark that she will find relevant and feasible under the circumstances. The discrepancy that he thus coordinates between what he and his listener believe promotes the behavior he desires only if she is unaware of the discrepancy—that is, as long as the "assumption of truth" still holds. While this process is assumed to be intentional in humans, similar strategic discrepancies can be described in animal communication without requiring terms such as "awareness" and "intention."

In some mixed-species flocks of feeding birds, for example, sentinel species give alarm calls that warn all members of approaching predators (Munn, 1986). A sentinel can also give an occasional "false alarm," which diverts a competing bird's attention from an insect that both are pursuing. This signal is effective because it alters the cognitive environment of the listener by evoking the relevant, and usually reliable, correlation between the signal and a predator. This change prompts a response appropriate for predator avoidance, but not for catching prey. On the other hand, the bird giving the false alarm is presumably operating from a different cognitive model in which not predator avoidance but a diverted competitor is the desired goal.

The sentinel, however, must budget its use of such false alarms, since the more often it uses them, the less effective they become. This is because repeatedly "crying wolf" sets up a different probability weighting for the signal-to-predator correlation in the competitor's mind. The sentinel must somehow keep track of when or how often this alternative strategy succeeds. Thus, as in the human example, a kind of "assumption of truth" must prevail, in the sense that more often than not, the signal must reliably correlate with the threat of a predator, for the deception to be effective.

The sentinel need not realize that it is coordinating such a discrepancy between its own representation of events and that of its competitor, for this

device to work. In fact, certain perpetrators of deception may have no cognitive representation of the situation whatsoever. Batesian mimics, for example, such as the palpable butterflies that have evolved wing patterns that mimic those of noxious species, have been "designed" by natural selection to conform to the "assumption of truth" rule. That is, such mimicry is an "evolutionary stable strategy" (Maynard-Smith and Price, 1973) only when the noxious butterflies sufficiently outnumber their palpable counterparts. This is because potential predators must be most likely to encounter the noxious variety if they are to learn to avoid all such butterflies. Evolution has managed to establish this coordination because, most of the time, it is beneficial for the predator to retain what it has learned—that is, to "assume" that the "truth" it has encountered in the past still holds.

VII. FLEXIBILITY AND COGNITIVE MANIPULATION

It is also built into learning systems, however, that such assumptions can sometimes be changed. After all, the natural world is always in flux—a particular food source may be depleted, familiar terrain may change, the status of cohorts may rise or fall. The more efficient an animal is at discriminating trivial from significant changes—the latter being those that warrant altering one's model—the less time and effort it is liable to expend meeting its needs (see Staddon, 1983). Thus, as suggested above, there is a clear evolutionary advantage to cognitive systems that can recognize and respond to relevant changes. It may likewise be advantageous to occasionally test for cues of such changes. In deception, for example, the potential victim may occasionally call the deceiver's bluff (e.g., van Rhijn and Vodegel, 1980). It is through such occasional testing of its expectations that the would-be victim acts as a stabilizing force on the coordination of strategies.

When the coordination of discrepant strategies involves two cognitive systems interacting, matters can rapidly become more complicated (see Byrne and Whiten, 1988). In that situation, a testing by one party becomes an important stimulus for the other party to observe and learn about. We then have a situation in which one of the relevant "truths" at issue in an interaction is not a noxious taste or other perceptual correlate. Instead, the relevant correlate with the testing signal is the signaler's state of mind, that is, its expectations or rather its challenging of them. As a result, selective pressure would arise for cognitive systems in which basic correlational machinery is sensitized to such indicators of cognitive events.

A particular caution is called for at this point on the part of those of us attempting to generate accurate models of the factors controlling animal behav-

ior. Signals, even "indicators of cognitive events," are themselves perceivable, physical events. Thus, there need not be a distinct cognitive mechanism for processing such signals as opposed to those that natural selection has "prearranged" in a given species. Thus, the "mind reading" discussed by Krebs and Dawkins (1984), while potentially subtle and complex, does not require qualitatively different cognitive processes from those involved in forming basic correlational models.

On the other hand, the more flexibility in the system generating the signals, the more sophisticated the interpreter needs to be to correctly identify relevant cues. Thus, the domain of communication can become the most complex and demanding of all the domains that a cognitive system has to model (see Jolly, 1966; Humphrey, 1986). This is in part a consequence of the fact that the concomitant complexity of the cognitive systems doing the modeling would make the process of coordinating such systems all the more demanding. One can see why even among cognitively complex animals such as primates, many stereotyped signals exist to reduce those demands and assure that at least some relevant information is not missed. But such animals may be capable of much subtlety and nuance their full range of communicative behavior. For this communication to be effective, interpreters must be able to recognize and respond to situations in which signals predict not just the likelihood of vital outcomes such as mating, eating, or fighting, but the cognitive preconditions for such outcomes as well.

In one example of this sort of prediction, Hinde (1981) discusses attempts to analyze the behaviors predicted by certain displays observed in avian conflicts. Particular displays, it turned out, could not be reliably correlated with the typical outcomes of attack, escape, or stay. Rather, they could only be said to predict possible *sets* of responses, such as "attack or stay" or "escape or stay." That is, "a given display does not have consistent sequelae" (p. 539). Thus, as a result of such variance, an animal attempting to use a simple correlational model would not be likely to effectively coordinate that model with its opponent's. Hinde suggests that the reason for this apparent ambiguity is that what the signaler will ultimately do depends, in part, on the further behavior of the other bird. The best each animal can do, then, in the course of such an interaction, is attempt to influence the other's model, and watch for indications of its resolution. Thus, again, we have a case of communication as *negotiation*, the terms of which, at least in part, are cognitive.

But, while maximizing such coordination is essential, it is also necessarily imperfect. As many critics of the "information sharing" perspective on communication have pointed out [Dawkins and Krebs (1978); but see Smith (1986)], it may not always be to an animal's advantage to reveal its true "intentions." Similarly, it may resist being manipulated to respond at a time or in a manner more advantageous to the other animal. These factors, along with the inherent

"noise" in such a system, make coordination particularly challenging. Nonetheless, it is this coordination that is most important—even more important—over the long run, than winning in any particular encounter. For successful coordination will not only enable the most confident attack but the wisest, risk-avoiding decision to flee when that response is most appropriate. This, then is a critical insight of the cognitivist approach: that a good deal of communicative behavior may be devoted not to actually eliciting a targeted response but to assessing and establishing the cognitive preconditions for a range of potentially relevant responses.

VIII. THE INFLUENCE OF RELEVANCE CONSTRAINTS

As should be clear by now, the cognitivist approach does not necessarily contest many fundamental intuitions of ethologists or predictions of sociobiology. What it can do is shift our orientation in such a way as to emphasize aspects of and approaches to the study of communication that might otherwise be obscured. In this final section, we will once more adopt the cognitive perspective and see what characteristics of communication are thrown into relief. While particular abilities vary, of course, from species to species, our above discussion of the coordination of cognitive systems suggests that there are certain general types of constraints in operation. These constraints—all factors in what an animal interprets as relevant—include the criteria by which information is sought, the importance of context, and the capacity to make use of pertinent stimulus relations.

IX. SEEKING INFORMATION

Much of the debate regarding the informational approach to the study of animal communication concerns whether signals have evolved to provide information. Various authors argue, for example, that senders may benefit from putting strategic limits on the information they make available through their signals. While it is generally accepted that seeking information is a primary goal for receivers [although see Dawkins and Guilford (1991) on the costs of receiving], senders are less often recognized as seekers of information. Of course, the same individual often alternates in the role of sender and receiver; however, while that individual is engaged in signaling, its concern is usually assumed to be which or how much information it is releasing. The cognitive perspective, however, suggests that senders can also be considered to be engaged in an act of seeking information when they signal.

That is, animals sometimes prospect for information with their signals. When an animal calls on its territory, it is not just sending out information about its presence, identity, status, etc. It is also using an effective technique for eliciting information about, for instance, who else is nearby. It may have learned this technique if, in the past, its calls were, at least under certain conditions, liable to be answered. (Alternatively, if the animal perceives a potential receiver that does not answer, this too can be informative; see section XI.) Greetings and solicitations likewise play the double role of announcing one's interests and determining the interest of others. Thus, the sender's communicative activity is aimed at manipulating the information made available to it.

Maynard-Smith and Price (1973), in one of the earliest applications of game theory to animal communication, suggested that a contestant will occasionally "probe" to determine if its opponent is willing to escalate a conflict. Such probes can also be used to verify the status quo, to call another's bluff as discussed above, or to otherwise test the social waters. Probes constitute an adaptive strategy for resisting exploitation by enabling "skeptical" communicators to demand additional information (Smith, 1986). They can also help to reduce the cost of signal assessment, such as the risk of predation during signal exchanges. They do this by allowing receivers to tolerate lower-cost but less reliable signals in a setting where occasional probes can be used to test for cheaters (Dawkins and Guilford, 1991). Whenever such probes are a function of an animal's expectations, they are a direct product of the current organization and demands of that animal's cognitive environment.

As described above, one function of a cognitive environment is to generate predictions. Such predictions not only establish a passive preparedness but are used to instigate behavior as well. If the "confidence levels" of these predictions are high, the animal may act in anticipation of the predicted outcome. However, such levels can fall below some threshold of action when the situation is changing rapidly, when similarity to previous experience is incomplete, when a direct violation of expectations is encountered, or when available information is otherwise ambiguous. In these cases, the cognitive system will work to highlight what sort of information is required for a more reliable analysis. As a result, the type of signal an animal sends can be fashioned less by what it has experienced in the immediate past than by what it predicts it will *need* to experience in the future.

For example, information-seeking is strongly motivated when an animal receives some indication that its expectations are in error. Labeled "surprise" by learning theorists, this phenomenon drives a search for information by peaking attention, increasing sensitivity to perhaps newly relevant stimuli, and facilitating rapid relearning. Suppose, for example, a blackbird, established on its territory and familiar with its neighbors, suddenly hears a strange voice. The bird will be motivated to find out more about this stranger: its sex, if it is just passing through, if it poses a threat, etc. Before the blackbird can decide what to do about the stranger, that is, decide which evoked behavior from the other would be

"desirable," it must update its representation of the situation. Thus, our interpretation of the blackbird's calls should not assume that they are aimed at controlling the situation; rather they may be designed to gain the epistemic ground from which it can exercise that control.

One important implication here, then, is that an animal's cognitive assessment of a situation creates not only estimates of its own optimal behavior and the desired behavior of others, but also a characterization of *what it needs to know.* Thus, at least some of its communicative effort will be designed to fulfill that need. A second factor comes into play, however, since evolutionary theory suggests that it may not always be in the interest of the other party to make this information available. This puts the first animal in the position of potentially benefiting from making use of collateral information. Both of these insights suggest that our interpretation of animal communication would benefit from a greater emphasis on context.

X. THE IMPORTANCE OF CONTEXT

A. Past Experience

Since historical context varies from individual to individual, ethologists concerned with general principles of communication may feel that their models should be independent of such particulars [although see Beer (1976); Smith (1977)]. However, there are certain general constraints on how past experience is accumulated and represented that can have a broad impact on how communication evolves.

One such capacity that influences communication is learning by observation (see Zentall and Galef, 1988). Many of an animal's most important lessons are learned by watching others (e.g., Losey *et al.*, 1986). Blackbirds, for instance, can learn to identify predators by observing the mobbing behavior of other flock members (Curio, 1988). Similarly, social learning has been shown to influence food preference in rats, apparently via olfactory cues from foragers that have returned to a central meeting place (Galef, 1988). This sensitivity to the behavior and condition of others clearly plays a role in communication as well. Not only does such a sensitivity facilitate the interpretation of signals, it also potentially brings the full range of observed behavior to bear in such interpretations.

One of the important "topics" of animal communication is "resource holding power" (RHP) (Parker, 1974). That is, many signals that animals produce serve as indicators (which may be more or less reliable, depending on a variety of factors) of a given individual's ability to control access to a valuable resource. Social learning becomes a factor in the impact of RHP-related signals when

observers can gain insight on the reliability of such signals from watching behavior that is not specialized for communication. Blackbirds, for instance, can watch fights between other conspecifics, to facilitate their assessment of the RHP of those birds (Freeman, 1987). These observations will influence the effectiveness of the fighters' subsequent signals because those signals will now be interpreted in light of the observer's preestablished representations of the fighter's true abilities.

Signalers can also exploit the capacity of receivers to bring their past experience to bear. That is, signals can be produced specifically to establish certain expectations on the part of the receiver. If, for example, a signaler establishes a certain *reputation*, it can exercise more control over how its subsequent signals will be interpreted. Such signals have been observed in mantis shrimp (Caldwell, 1986), for example, which act primarily aggressively just before molting. Immediately after a molt, these shrimp are especially vulnerable to attack; the reputation they establish before the most increases the likelihood that their subsequent charade of competence will be taken at face value.

Notice that this sort of strategy works only when the signaler is likely to repeatedly encounter the same challengers—challengers that can learn from the aggressive signals and that will remember them (at least long enough for the signaler to recover from its molt). In animals with much longer memories and more subtle capacities for bluff and detection, signals that establish and test such reputations are liable to be similarly subtle and complex. In fact, it has been proposed that pressures exerted by the demands of increasingly complex communication may account for the evolution of "intelligence" in higher mammals, including humans (see Humphrey, 1976, 1986; Byrne and Whiten, 1988; Johnson, 1990; Donald, 1991).

In this context, "intelligence" refers to a sophisticated capacity for representation that enables an animal to be especially flexible in applying what it has learned to novel situations. Such representations, for example, may enable an animal to calculate the likelihood of success of deceptive signals based not on past experience with a given individual but on aspects of that individual's behavior that bear certain categorical similarities to that of other successfully deceived cohorts. That is, if an animal is capable of representing another's behavior not in terms of specific, perceptual correlates, but in more "abstract" terms, such as relative to certain motives or goals, it may be able to learn which of its own signals tend to be effective in countering or promoting such goals. Thus, it would be capable of moving beyond the use of either relatively hard-wired strategies (as in the shrimp, above) or simple correlations, in familiar situations, of signals with particular behaviors. Instead, the intelligent animal would be able to make use of its past experience in ways that depend critically on how it *construes* those experiences (see Johnson, 1990). Although it may be virtually impossible to determine, by naturalistic observation alone, when an animal is employing such

representations [for an excellent discussion, see Cheney and Seyfarth (1990, Chapter 8)], continued work under controlled conditions in the lab may provide insight into the intellectual capacities of various species and how they may impact on communication abilities.

B. Current Context

The most obvious context of importance to communication is the audience. In recent research on audience effects, Marler and his colleagues (Marler *et al.*, 1986), for example, demonstrated that chickens can modify their signals depending on the appropriateness of the available audience. In particular, they found that cockerels were more likely to give alarm or food calls, in the presence of a predator or food source, when their mates were present. Females of other species, other male chickens, and even hens with chicks were not as "inspiring" as audiences for such calls.

One issue that is raised by such research concerns how animals discriminate which sorts of audiences are relevant. That is, to appropriately assess such behavior, we need to know something about how the species in question categorizes the stimuli in its environment. If learning were confined to the representation of only previously encountered stimuli (or even of those stimuli and associated responses) each novel experience would demand the full deployment of learning resources. But, even in simple organisms, strategies such as stimulus generalization enable animals to generate reasonable responses to similar, but different, stimuli. As cognitive complexity increases, such similarity judgements can be based on a wide variety of dimensions and the same stimuli can even be classified into different categories depending on the demands of the moment. Knowing something about the parameters by which a species can classify its environment has an obvious bearing on our understanding of communication in that species.

Cheney and Seyfarth [(1990); see also Seyfarth and Cheney (1986, 1988)], for example, in their work with vervet monkeys, have investigated the relationship between the monkeys' categorization abilities and how they produce and respond to signals. This research has shown, for instance, how the development of a young vervet's ability to use predator-specific alarm call reflects an increasingly precise categorization of dangerous versus unthreatening passersby (Seyfarth and Cheney, 1986). They have also discovered that when a (relatively unreliable) infant gives an alarm, nearby adults will look to that infant's mother for confirmation of the danger, revealing how classification by familial relations influences information-seeking behavior (Cheney and Seyfarth, 1982; see also, Dasser, 1988). They have also shown that while environmental information on social (i.e., neighboring vervet troops) versus nonsocial events (i.e., neighboring "irrelevant" hippos) may be equally available, the vervets have a sensitivity to

learning only from the relevant social cues (Cheney and Seyfarth, 1985). Knowledge about the capacities of other animals to discriminate and classify events could likewise lead to insights about the domains in which their signals operate (see, for example, Gouzoules *et al.*, 1974; Dasser, 1988).

XI. REPRESENTING RELATIONS

Once we start thinking in terms of context, our typical portrayal of communication as a sequence of alternating activity by a signaler and a receiver begins to blur. The traditional "alternating sequence" model offers the advantage of examining communication from the perspective of an individual, the most widely recognized unit of selection. It also corresponds to a common pattern of (especially acoustic) signal production, in which animals take turns signaling and attending. However, not all communication involves roles so clearly delimited in time. Even when it does, a description in which a *set of communicative events are taken as the fundamental unit of communication* can yield valuable insights hidden from the sequence perspective.

This level of analysis is justified when we recognize that memory allows two signals to be represented simultaneously in an animal's mind. As a result, the separate production of these signals may not always be an important feature in their interpretation. It is generally assumed that signals exert their effects through the recognition of their structure by receivers. But there is a danger in assuming that the "message" in animal communication is always carried in the structure of a signal. When an animal has the ability to remember and compare signals, both those it has made and those it has perceived, not only signals but *the amount and type of difference between them* can carry important information. Cognitive systems, even the simplest ones, are especially good, via generalization, similarity gradients, matching functions, etc., at determining how alike or different stimuli are.

Such processes no doubt play a role, for example, in the roaring of red deer (Clutton-Brock and Albon, 1978). Contests between male red deer escalate from bouts of relatively low-level calling to competitions over which can roar the longest and loudest. Much discussion has centered around the issue of whether each deer's roars are a "honest" advertisement of his strength and tenacity. But this focus on the individual's evolutionary advantage (or disadvantage) once again ignores the means to that end. A particular roar of a given loudness does not, in itself, convey the important information. What matters is whether that roar is louder than the one to which it is an answer. That is, it is the relation between roars that tells the animals where they stand in this contest.

The cognitive processes that underlie such an assessment of signal relations

can foster much more than the relatively fixed exchanges that characterize court-ship and combat rituals. They also enable great variation in how and what is interpreted as a communicative act. This is what allows silence, for instance, to serve as a "loud and clear" signal. If, for instance, an animal, for whatever historical or situational reasons, expects another to vocalize, but that second animal remains mute, the contrast between the silence and the expected call can be an informative relation. Similarly, suppose one animal is quietly eating and is approached by another with a lively invitation to play. If the receiver continues eating, that act conveys a message because of its relation to the expectation in the signaler's (and probably in the receiver's) mind. Thus, cognitive processes are an especially important factor here.

On a slightly different tack, suppose one animal produces a sound and another mimics it. Regardless of the "referent" (Smith, 1986) of the sound—be it an alarm, a greeting or a challenge—the fact of similarity between the two animals' signals conveys an additional message not carried by the structure of either signal. The sameness of signals communicates "togetherness"—an align-ment of two animals' attention, a likelihood of continued interaction. This mes-sage is available not only to the participants themselves but to any observers as well. Although in some sense independent of the particular signals involved, this sameness is registered as a relevant aspect of the display, an aspect that in itself can be correlated with subsequent important events.

A coalition of male dolphins, for instance, will cruise in a tight formation, making sudden changes of direction in perfect synchrony. For whatever else this activity signals, the sameness of the behaviors certainly makes clear that these males are a "unit," ready and able to act together. As such, they present a formidable defensive force to potential predators or an intimidating show to a competing group of males, either of which may impress an observing female. Such synchrony may also test the ability for an aspiring coalition partner to maintain the high level of coordination that may be necessary during food gather-ing or defense. Whether the animals are synchronously surfacing, leaping, div-ing, or making sharp turns, the sameness of these behaviors can be cognitively represented and become an additional source for generating relevant predictions.

The use of the relation of sameness between signals can be formalized by evolution, as in the courting duets of many birds. The synchrony or carefully timed antiphony of such calls can, for instance, produce hormonal responses that promote successful reproduction. But these strategies can also be used in more flexible interactions, as in the duets of gelada baboons (Richman, 1987). A male baboon may compose a novel "song"—a call a few phrases long—which it will repeat in the presence of (what he is trying to ascertain as) "his" females. He will then abruptly halt his calling near the end of a song, and expect a female to complete the final phrase. In this way he can test whether she has been attending closely enough to learn the simple song, as well as to produce its ending at the

appropriate time. What makes her vocalization relevant, that is, what accomplishes their, in this case, mutual goal, is not the nature of the signal itself but the fact of its relation to the prototype that the male has produced.

In light of our above discussion of animals' abilities to discriminate and categorize stimuli in their environment, signal relations open a wide field of possibilities for this level of analysis. Depending on the criteria by which an animal can represent the similarity or difference of various signals, a great deal of "relevant" information may be available in animal exchanges of which we have little inkling. In humans, even sticking to the same conversational topic is a way of signaling "togetherness," whether the interlocutors agree or disagree. If such subtleties are ever to be understood by those of us observing animal interactions, we may need to shift our own estimates of what abilities are "relevant" to a comprehensive study of animal communication.

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