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The Cognitive Animal

Empirical and Theoretical Perspectives on Animal Cognition

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39 Cracking the Code: Communication and Cognition in Birds

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Since monkeys certainly understand much that is said to them by man, and when wild, utter signal-cries of danger to their fellows; and since fowls give distinct warnings for danger on the ground, or in the sky from hawks . . . may not some unusually wise apelike animal have imitated the growl of a beast of prey, and thus told his fellow-monkeys the nature of the expected danger? This would have been a first step in the formation of a language. . . . When we treat of sexual selection we shall see that primeval man, or rather some early progenitor of man, probably first used his voice in producing true musical cadences, that is in singing, as do some of the gibbon-apes at the present day; and we may conclude from a widely-spread analogy, that this power would have been especially exerted during the courtship of the sexes,—would have expressed various emotions, such as love, jealousy, triumph,—and would have served as a challenge to rivals. (Darwin 1871, pp. 56–57)

Charles Darwin clearly believed that language had evolved from precursors in the natural signals of animals. As with so much of his writing, these passages anticipate recent research programs. He points out that monkeys and chickens have distinctive alarm calls for different kinds of danger, and goes on to suggest that language is the product of sexual selection. Darwin's argument is a case for continuity.

Over a hundred years later, this idea is still treated with considerable skepticism (e.g., Premack 1975; Luria 1982; Wallman 1992; Lieberman 1994). Critics typically take the Cartesian position that language is special, in the sense that all of its attributes are unique to humans. It follows that comparative studies should fail to reveal any comparable traits in nonhuman animals. These reservations are often summarized in two related assertions: First, that animal signals are simply a readout of emotional state and second, that their production is reflexive or involuntary. The resolution of this controversy is important because if Darwin was right, then we can use communication as a window on the

minds of nonhuman animals. Evidence for continuity would also force us to re-think assumptions about the nature and extent of human uniqueness.

My research program focuses on the relationship between acoustic signaling and cognition in birds. I have adopted an ethological approach (Tinbergen 1963), choosing to study natural behavior of obvious functional importance. The techniques used include both controlled laboratory experiments to characterize mechanisms and studies of social groups under natural conditions to obtain insights about function. The theoretical assumption underpinning this work is that cognitive processes are adaptations in just the same way as physical structures.

Referential Signals

The first evidence that animal communication might be more complex than traditional models had anticipated came from Struhsaker's (1967) pioneering field studies of vervet monkeys (*Cercopithecus aethiops*). This work established that vervets have acoustically distinct alarm calls corresponding to their three principal classes of predator: eagles, leopards, and snakes. Seyfarth and Cheney followed up this work with playback experiments, convincingly demonstrating that calls are sufficient to evoke responses appropriate to the type of predator that had originally elicited the sound (Seyfarth et al. 1980). Macedonia's (1990) studies of ring-tailed lemurs (*Lemur catta*) provide similar evidence of predator class-specific alarm calls.

Vervets and lemurs have referential signals. In both species, identifiable external events reliably elicit a particular type of call and these signals are sufficient to evoke adaptive responses, even when contextual cues are unavailable. The strategy for exploring the characteristics of any sys-

tem of referential signals involves mapping these relationships between eliciting conditions and signal structure, and between signal structure and receiver's response (Marler et al. 1992; Evans and Marler 1995; Evans 1997).

I am fascinated by the challenge of understanding the information encoded in animal signals. My subjects are golden Sebright chickens, an ornamental strain closely related to the ancestral red junglefowl (*Gallus gallus*). These birds have a large vocal repertoire (Collias 1987), which does not seem to have been altered by domestication. Most important, they have two distinct types of alarm call. A particular advantage of working with chickens is that they tolerate captivity well. It is thus possible to analyze quite precisely the conditions under which alarm calls are produced by presenting simulated predators and manipulating their characteristics.

The subjects in these laboratory experiments are males because aerial alarm calling is testosterone dependent (Gyger et al. 1988). Individual roosters are confined in a cage with a large video monitor supported on a frame overhead so that the screen is horizontal and facing downward (figure 1 in Evans and Marler 1992). Most of the time the monitor displays a blank white field, but periodically computer-generated animations of raptors can be triggered so that they fly across the screen. A second monitor at ground level allows footage of terrestrial predators to be presented. These video sequences evoke the full gamut of antipredator responses (figure 1 in Evans et al. 1993a). In early experiments, we showed the birds fast-moving hawk silhouettes overhead and an edited sequence of a walking raccoon (*Procyon lotor*) at ground level and found that there was an unambiguous relationship between alarm call and predator type with these prototypical stimuli. Only aerial alarm calls were evoked by the hawk animation and only ground alarm calls were evoked by the raccoon footage (Evans et al. 1993a).

One possible explanation for this finding was that alarm call type might simply reflect the

spatial location of a stimulus. We assessed this idea by digitizing video sequences of a soaring hawk and of the raccoon and then editing them frame by frame to remove the background. This ensured that comparisons between the predator types would not be confounded by the settings in which they had been filmed. We then showed males the isolated hawk and raccoon, presenting each of them at ground level and overhead.

The results replicated our original demonstration that only aerial alarm calls are given in response to a raptor presented above and only ground alarm calls to a terrestrial predator in the normal position. The hawk at ground level and raccoon overhead both evoked a mixed response, but each of these stimuli was significantly less effective than the hawk overhead (figure 15.6 in Evans and Marler 1995). Evidently placing a terrestrial predator overhead is not sufficient for the birds to treat it as an aerial predator. On the other hand, spatial location clearly plays a role, because the number of calls elicited by both types of predator was reduced when they were in inappropriate positions. Unfortunately, this experiment has been misinterpreted as evidence that chicken alarm type is entirely determined by the location of the threat (Zuberbühler 2000). Neither the data nor our original description of this study (Evans and Marler 1995) logically supports such a conclusion.

Next, we turned to the question of specificity, concentrating on aerial alarm calls. What constitutes an adequate stimulus? Would any moving object do, or are alarm calls triggered only by potential predators? Experiments explored the importance of simple parameters such as apparent size, speed, and shape. We used computer-generated animations so that we could define stimulus attributes precisely; a single characteristic could be manipulated while all others were held constant. The speed continuum covered the full range that a bird would be likely to experience under natural conditions, from the leisurely movement of a vulture soaring on a thermal at one end, to the speed of an attacking harrier at

the other. Similarly, the apparent size of hawk shapes (expressed in degrees subtended at the bird's eye) was varied from 1 to 8°, a range known to be associated with variation in alarm calling during natural encounters with potential predators (Gyger et al. 1987). Stimulus shape was manipulated by using a morphing algorithm to create a continuum from a disk to a realistic silhouette of a red-tailed hawk.

This series of experiments allowed us to define in some detail the characteristics of events that chickens respond to with aerial alarm calls. The most effective stimuli were found to be overhead (Evans and Marler 1995), large (apparent size > 4°; Evans et al. 1993b), fast-moving (apparent speed > 7.5 lengths/second; Evans et al. 1993b), and approximately bird shaped (Evans and Marler 1995).

Studies of signal production thus show that chickens have two distinct types of alarm call, each associated with a different class of predator, and that aerial alarms at least are evoked by a relatively specific subset of possible stimuli. What about signal receivers—are these sounds sufficient for selection of an appropriate response? To find out, we played both types of alarm call to isolated hens confined in a cage, with a small area of brush to provide cover. Hens responded to ground alarm calls by drawing themselves up into an unusually erect “alert” posture, becoming more active and scanning back and forth in the horizontal plane, as though trying to detect a threat approaching on the ground. When they heard aerial alarm calls, they reacted quite differently, running to cover and then crouching with their feathers sleeked and looking upward, precisely as though they were trying to detect an object moving overhead. Each of these responses is appropriate to the type of predator that originally elicited the call. We concluded that chicken alarm calls, like those of vervets and lemurs, are referential signals (Evans et al. 1993a).

Predators are not the only environmental events that chickens respond to with distinctive

calls. Consider the social interaction depicted in figure 39.1. The male has found a food item and is producing characteristic pulsatile sounds, known traditionally as food calls (Collias and Joos 1953). A hen has responded by approaching and is now fixating closely on the fragment of grass in the male's beak. The male will typically then let the hen have the food, either by dropping it on the ground in front of her or by allowing her to take it directly from between his mandibles.

There are two types of explanation for this behavior. One possibility is that hens approach because food calls provide quite specific information about feeding opportunities (Marler et al. 1986). Alternatively, food calls might not really be “about” edible objects at all, but rather describe the subsequent behavior of the sender (Smith 1991), in which case hens would respond to these sounds because they predict a low probability of aggression. To distinguish between these accounts, we needed to study production of food calls. Are they dependent upon the availability of food, or are they just given by friendly males?

We used simple instrumental conditioning techniques to train roosters to peck a key for periodic deliveries of small food pellets (Evans and Marler 1994). During the first 2 minutes of each test session, the key was unlit and pecks delivered to it had no effect; then it was switched on, signaling that food was available. The results of this simple manipulation revealed that food calling is indeed dependent upon the presence of food items and cues reliably associated with them. When the key was first lit, the rate of food calling increased by an order of magnitude, then dropped slowly as the males become satiated. Tests with a hen confined in an adjacent cage also showed that there was no temporal relationship between food calling and courtship behavior (Evans and Marler 1994). These results demonstrated that there is a predictive relationship between food availability and production of food calls by males, which is incompatible with the idea that these sounds reveal only the subse-



Figure 39.1

Typical interaction between a food-calling male golden Sebright chicken and a hen. Note close inspection of the food item by the female.

quent behavior of the sender, although it is likely that this information is also encoded.

The next study considered the receiver's point of view. Studies of call production suggested that food calls might signal feeding opportunities, but in a natural interaction hens have lots of other information available to them. Roosters are not only calling, but also performing stereotyped 'tidbitting' movements in which they pick up and drop the food item repeatedly (figure 39.1). Females can clearly see these visual signals and also perhaps the food itself. To determine whether food calls alone are sufficient to explain the hens' responses, we needed to conduct playback experiments in which all of these other cues were stripped away.

Our first study compared food calls with ground alarm calls, which have similar acoustic characteristics. The second series of playbacks compared food calls with contact calls, which are also produced during affiliative social interac-

tions, and are hence matched for the subsequent behavior of the sender. Hens responded to recorded food calls by moving about the cage, pausing repeatedly to fixate on the ground in front of them. There was no such increase in substrate-searching behavior when ground alarm calls were played back. Even though these two sounds are structurally similar, they have qualitatively different effects on the hens' behavior, and these reflect the different circumstances under which the calls are produced (Evans and Evans 1999). Contact calls also had no effect on the duration of substrate searching. This result demonstrates that the effects of food calls are quite specific and suggests that the behavior of hens is mediated by the likely availability of food, rather than a desire to approach a non-aggressive companion (Evans and Evans 1999).

Taken together, these laboratory studies of alarm calling and food calling reveal a perhaps surprising degree of communicative complexity.

Other work, which I will not describe in detail here, shows that production of these calls is not simply dependent upon the eliciting stimulus (food or predators) but is also sensitive to the presence of appropriate receivers (Evans and Marler 1991, 1992, 1994). Such audience effects are consistent with a degree of volitional control.

Communication and Cognition

The acoustic signals of birds are thus substantially more sophisticated than most theorists have anticipated (Evans and Marler 1995; Evans 1997). The same is true of the alarm calls of primates (Cheney and Seyfarth 1990). Such signal systems do not, however, necessarily require us to postulate complex cognitive underpinnings; there are several alternative interpretations.

Consider vervets giving snake alarms to an approaching python. Their system, like those of chickens, has the following properties: One type of call (X) is reliably elicited by a specific class of environmental events (Y), and presentations of X are sufficient to evoke responses adaptive for dealing with Y .

How are we to interpret such observations? One possibility is that the alarm call is semantic, or representational—it tells companions specifically “There is a Y ” (Cheney and Seyfarth 1990). But other interpretations cannot be excluded. Call X might reflect a Y -specific internal state (‘snake fear’; Premack 1975; Lieberman 1994). Alternatively, it might not have an external referent “snake,” but rather a behavioral referent that describes the subsequent actions of the sender (“I’m going to stand bipedally and peer into the grass”; Smith 1991). Finally, we have the interpretation favored by Baron-Cohen (1992) and Wallman (1992): Call X is instructive. It tells companions “Quick! Look down!”

Any claim for languagelike attributes in the natural signals of animals depends critically upon underlying cognitive processes. It requires that call X really be representational. Each of the other three possibilities produces the same be-

havioral output, but in these cases the parallel with language is illusory. This is why some theorists remain skeptical about the degree of continuity implied by the contemporary literature on referential signaling.

It has been challenging to distinguish among these models because the problem does not seem at first to be experimentally tractable. Some years ago, Joe Macedonia and I suggested that it might be best to adopt a neutral stance, acknowledging the constraints on interpretation of observations and playback experiments; studies like those that I have discussed so far demonstrate only that call X is functionally referential—receivers behave *as if* it predicts a class of environmental events (Macedonia and Evans 1993). Early attempts to grapple with this problem empirically in the vervet system (Cheney and Seyfarth 1988, 1990) provided only weak evidence for semantic properties (Evans 1997), but there is now agreement that the central issue is whether referential signals have their effects by evoking representations of the eliciting event.

Representation is a special word in psychology, cognitive science, and linguistics, so it is important to explain my use of it here. Consider the relationship between football jersey numbers and player identity, a simple example borrowed from Gallistel (1990). Mapping between these systems is systematic and constrained in two ways: First, assignment is one-to-one (each player can only wear a single number). Second, numbers are unique (the same number cannot be given to more than one player). These rules define a functioning isomorphism between the number system and the individual identity system.

There is a clear parallel between this type of mapping operation and the use of “representation” in neural networks, where it denotes the relationship between input values and a pattern of nodal activation. This general usage in psychology has a long history; it can be traced back at least as far as William James (1890), who speculated along the same lines about the relationship between stimuli and brain activity.

Gallistel (1990) calls representations of this type “nominal representations.” He places them at the lowest level in a hierarchy of increasingly complex types of representation, characterized by the computational operations required to derive them. Gallistel considers nominal representations impoverished because the only operation that they can compute is *equals to* or *identity*. But such operations are functionally important. Animals frequently have to test for a match between stored information and a stimulus that they have encountered, and often the decisions made as a consequence of such processes really matter. For example, birds can learn to avoid insects with warning coloration after a single unpleasant experience. Each subsequent encounter is effectively a matching-to-sample task, requiring comparison with stored information about morphology.

In some systems we can be confident that adult behavior reflects the acquisition of representations during development. Oscine birds acquire a detailed model of song while they are still nestlings and reproduce it as adults (including all of the nuances of the local dialect) by matching their own output against this template. Exploration of the specialized systems necessary for this feat has been one of the most successful paradigms in neuroethology (Marler 1990; DeVoogd 1994). A similar point can be made about filial imprinting. Elegant experiments by Bateson, Horn, and their colleagues have shown that storage of information about an imprinting object (in nature this would be the mother’s face) involves centers in the chick’s left forebrain; this process is now understood at the cellular level (Horn 1990; Honey et al. 1995).

There is hence no doubt that animals have representations. Indeed, they may prove to be ubiquitous. What is contentious is whether they are involved in communication. To make this question specific, and thus testable, let us return to chicken food calls and ask how we might explain the characteristic substrate-searching response of a hen. There are two distinct possibilities. The call might evoke looking downward directly by triggering the appropriate motor pat-

tern. Alternatively, food calls might stimulate retrieval of stored information about food, which then determines the hen’s response. In the absence of additional evidence, we might prefer the reflexive account for reasons of parsimony.

To address this problem, we chose a strategy based upon classical work in associative learning which established that behavior is influenced by stored information about reinforcer properties (reviewed by Shettleworth 1998). The general approach in these studies was to explore the effects of manipulating one class of environmental events. Animals were trained to associate two distinct stimuli with two different types of reinforcer. Then one reinforcer, but not the other, was selectively devalued, either by pairing it with a toxin or by satiation. This caused a change in response that was specific to the stimulus associated with the devalued reinforcer, demonstrating that the animals had formed separate representations for each of the two rewards (Colwill and Rescorla 1985; Holland 1990; Hall 1996). Results of this kind are incompatible with the idea that responses to conditioned stimuli are entirely reflexive; they require us instead to postulate simple cognitive processes.

The logic of our design was closely analogous. We reasoned that if chicken food calls encode information about feeding opportunities, then responses evoked by playback should be affected by prior experience of food. Such a change in responsiveness should be highly specific; responses to another, similar, call type should be unaffected. Neither of these predictions is generated by alternative nonrepresentational models of call processing by the receiver.

Ground alarm calls were selected as a control because, as indicated, they closely match the acoustic structure of food calls, but have very different eliciting conditions. During test trials, calls were played back to hens either 3 minutes after delivery of a small quantity of food (three fresh corn kernels), or without such a pre-playback experience. The critical planned comparisons tested for an interaction between pre-playback experience and signal type.

The effects of manipulating prior access to food selectively changed responses to food calls, exactly as predicted by a representational model (Evans and Evans, in review). Playback of food calls evoked anticipatory feeding behavior, but only when this had not been preceded by a food delivery. In no-food trials, hens responded to food calls by searching the substrate significantly more than in trials with matched ground alarm calls. This difference was abolished by allowing a brief feeding bout before playback of the call. Our interpretation is that under these conditions, the signal provided no new information. In contrast, the response to ground alarm calls was entirely unaffected by prior experience of food. These results demonstrate that chicken food calls do not affect the behavior of companions by evoking motor patterns in a reflexive way. Rather, they stimulate access to a representation of food.

Recently completed experiments with alarm calls have produced precisely comparable results; responses are selectively changed by prior experience of the corresponding predator type. We conclude that chicken calls produce effects by evoking representations of a class of eliciting events. This finding should contribute to resolution of the debate about the meaning of referential signals. We can now confidently reject reflexive models, those that postulate only behavioral referents (Smith 1991), and those that view referential signals as imperative (Baron-Cohen 1992; Wallman 1992). The humble and much-maligned chicken thus has a remarkably sophisticated system. Its calls denote at least three classes of external objects. They are not involuntary exclamations, but are produced under particular social circumstances.

Clearly, representational signaling is not restricted to our closest primate relatives (see reviews by Hauser 1996; Shettleworth 1998). One of the major challenges for the future will now be to identify the ecological and social factors responsible for the evolution of such systems. The insights obtained will integrate studies of cognition more closely with those of function.

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