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The Cognitive Animal

Empirical and Theoretical Perspectives on Animal Cognition

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Monkeys and apes live in complex social groups and must master a formidable calculus if they are to survive and reproduce. Baboons' groups, for example, are often composed of 80 or more individuals drawn from 8 or 9 matrilineal families arranged in a linear dominance rank order. What sort of intelligence is required to navigate this social landscape? How do individuals acquire information about their companions, and how do they store it in memory? Such questions are interesting because understanding social relationships and predicting behavior may have been the most complex problems faced by our ancestors during periods when the human brain increased most dramatically in size. Some authors have even suggested that human intelligence evolved largely because selection favored individuals who could solve complex social problems (Jolly 1966; Humphrey 1976; Cosmides and Tooby 1994).

Research on the mechanisms that underlie primate social intelligence is, however, fraught with problems, largely because the behavior of monkeys and apes can be explained equally well in many different ways. Does a baboon that apparently knows the matrilineal kin relations of others have a "social concept," as some have argued (e.g., Dasser 1988), or has the baboon simply learned to link individual *A1* with individual *A2* through a relatively simple process like associative conditioning, as others believe (e.g., Thompson 1995)? At present, the preferred explanation often depends as much upon the scientist's mind as upon any objective understanding of the baboon's.

Our research is conducted in the field, among nonhuman primates living in their natural social groups. We use long-term observations and videotaped playback experiments to address the question: What must a monkey know, and how must its knowledge be structured, in order to account for its social behavior? Our goal is to

develop models of social intelligence that account for existing behavior and that explain why, during the course of primate evolution, some cognitive strategies have been favored over others.

Knowledge of Other Animals' Kin Relations

East African vervet monkeys (*Cercopithecus aethiops*) live in groups of 8–30 individuals. Females remain throughout their lives in the group where they were born. When males are 5–6 years of age, they emigrate to a neighboring group. Adult females and their offspring can be arranged in a linear dominance hierarchy, with offspring ranking immediately below their mothers. The stable core of a vervet social group is thus a hierarchy of matrilineal families (Cheney and Seyfarth 1990).

Most friendly interactions, such as grooming and the formation of aggressive alliances, occur within families (reviewed in Cheney and Seyfarth 1990). Clearly, individuals distinguish their own matrilineal relatives from all others because their behavior toward them is so different. There is also evidence, however, that vervets recognize the close associates of other group members (Cheney and Seyfarth 1986; Harcourt 1988). For example, a vervet who has been involved in an aggressive interaction with a particular opponent will often soon afterward threaten a close relative of the opponent. Knowledge of other individuals' social relationships can only be obtained by attending to interactions in which one is not involved and making the appropriate inferences.

Studying vervet monkeys in Amboseli National Park, Kenya, we taperecorded the vocalizations given by known individuals in social interactions with one another. In a series of playback experiments, we then played the distress scream of a juvenile to a group of three adult females, one of whom was the juvenile's mother.

The females' responses were filmed. As expected, mothers looked toward the loudspeaker for longer durations than did control females. Even before she had responded, however, a significant number of control females looked at the mother. They behaved as if they recognized the link between a particular vocalization, a specific juvenile, and a particular adult female (Cheney and Seyfarth 1980, 1982).

In a more recent study of baboons (*Papio cynocephalus ursinus*) in the Okavango Delta of Botswana, two unrelated females heard a sequence of calls that mimicked an aggressive interaction between two other members of their group. The first sequence mimicked a fight between two individuals who were both unrelated to either female. Neither subject responded. The second sequence mimicked a fight between a relative of the dominant subject and another, unrelated individual. The subordinate responded by looking at the dominant. The third sequence mimicked a fight between one of the dominant's and one of the subordinate's relatives. Both females responded by looking at each other (Cheney and Seyfarth 1999). Moreover, after hearing this third sequence, the two females were more likely to be involved in an agonistic interaction than after hearing either of the two other sequences. Apparently, baboon females view their social groups, not just in terms of the individuals that comprise them, but also in terms of a network of social relationships in which certain individuals are linked with several others (for further discussion, see Seyfarth and Cheney in press).

Knowledge of Other Animals' Dominance Ranks

Along with matrilineal kinship, linear, transitive dominance relations are a pervasive feature of social behavior in groups of Old World monkeys. A rank order might emerge because individuals can recognize the transitive dominance relations that exist among others: *C* knows that

A is dominant to *B*. Alternatively, monkeys might simply recognize who is dominant or subordinate to themselves. In the latter case, a transitive, linear hierarchy would be an incidental outcome of paired interactions. The hierarchy would be a product of the human mind, not the minds of the monkeys themselves.

There is evidence, however, that monkeys do recognize the rank relations that exist among others. For example, dominant female baboons often grunt to mothers with infants as they approach the mothers and attempt to handle their infants. The grunts seem to function to facilitate social interactions by appeasing anxious mothers, because an approach accompanied by a grunt is significantly more likely to lead to friendly interaction than an approach without a grunt (Cheney et al. 1995b).

Occasionally, however, a mother will utter a submissive call, or "fear bark," as a dominant female approaches. Fear barks unambiguously indicate subordination; they are never given to lower-ranking females. To test whether baboons recognize that only a more dominant animal can cause another individual to give a fear bark, we played to adult females a causally inconsistent call sequence in which a lower-ranking female apparently grunted to a higher-ranking female and the higher-ranking female apparently responded with fear barks. As a control, the subjects heard the same sequence of grunts and fear barks made causally consistent by the inclusion of additional grunts from a third female who was dominant to both of the others. For example, if the inconsistent sequence was composed of female 6's grunts followed by female 2's fear barks, the corresponding consistent sequence might begin with female 1's grunts, followed by female 6's grunts and ending with female 2's fear barks. The subjects responded significantly more strongly to the causally inconsistent sequences, suggesting that they recognized not only the identities of different signalers but also the rank relations that existed among others in their group (Cheney et al. 1995a).

Evolution

How does an individual benefit from knowing the relations that exist among others? Current hypotheses stress the importance of triadic alliances, which occur whenever two or more individuals join together in directing aggression against a third. While alliances occur in many species, only primates (and perhaps dolphins, see Connor et al. 2000) appear to be strategic in their choice of alliance partners (Harcourt 1988). In macaques, for example, males consistently solicit allies who outrank both themselves and their opponents (Silk 1999). If alliances play an important role in competitive interactions, and if alliances only succeed when the solicitor recruits an ally who outranks and will not join his opponent, then solicitors must know the relative ranks and kin relations of all possible allies and opponents. In other words, they must know about the relations that exist among others.

Underlying Mechanisms

Humans readily divide social companions into groups and organize these groups within a hierarchical structure. There is, however, no a priori reason to believe that the same mental operations underlie social knowledge in monkeys and apes. Several authors, for example, have argued that primate social behavior can be explained by relatively simple processes of associative learning and conditioning (Heyes 1994; Thompson 1995).

Schusterman and Kastak (1993, 1998; see also chapter 28 in this volume) taught a California sea lion, Rio, to group seemingly arbitrary visual stimuli into equivalence classes. She learned to associate, for example, $A1$, $A2$, and $A3$, even though they shared no physical features. Next, Rio was rewarded for selecting stimulus $A1$ over stimulus $B1$. Finally, Rio was tested to determine whether she had begun to treat all A stimuli as equivalent to each other and all B stimuli as equivalent to each other, at least insofar as they

followed the rule *if $A1 > B1$ then $A_n > B_n$* . Rio performed significantly above chance.

The authors suggest that the kind of equivalence judgments demonstrated by Rio constitute a general learning process that underlies the recognition of social relationships in many species. Thus, for example, a baboon or vervet monkey learns to group members of the same matriline together because they share a history of common association and functional relations. And when one monkey, upon hearing a juvenile scream, responds by looking at the juvenile's mother, she does so because members of the same matriline have effectively become "interchangeable" (Schusterman and Kastak 1998).

There is no doubt that associative processes provide a powerful and often accurate means for animals to assess the relationships that exist among different stimuli, including members of their own species. Indeed, it seems unlikely that a monkey could form a concept such as "closely bonded" without attending to social interactions and forming associations between one individual and another. To some extent, learning about other individuals' social relationships is by definition dependent on some form of conditioning. However, before concluding that all primate social knowledge can be explained on the basis of learned contingencies (Heyes 1994), we note several ways in which equivalence class relations fail to capture the complexity of primate social relations.

Equivalence classes are typically based on a single underlying association, such as spatial or temporal juxtaposition. By contrast, no single behavioral measure is either necessary or sufficient to define the association among individuals in a primate matriline. A mother and her infant son interact in ways very different from those of two subadult male brothers, yet all four may be recognized by others as part of the same kin group.

While the stimuli that make up an equivalence class are mutually substitutable (Schusterman and Kastak 1998), the individuals that form a

matrilineal kin group are linked in more variable and less predictable ways. If infant baboon *A1* and juvenile baboon *A2* both associate at high rates with the same adult female and she associates with an adult male “friend” (Smuts 1985; Palombit et al. 1997), it would be correct to assume that the male is closely allied to the infant but incorrect to assume that he is equally closely allied to the juvenile.

Further complicating matters, individual primates belong to multiple classes simultaneously. An adult female baboon, for example, belongs to a matrilineal kin group, associates with one or more adult males, holds a particular dominance rank, and may be weakly or strongly linked to other females outside her matriline. The natural situation is considerably more complex than laboratory studies of equivalence classes.

Next, consider the problem of training. In Schusterman and Kastak’s experiment, as in many other studies, the subject was first presented with stimuli that had links to one another (*A1*, *A2*, *A3*) and then rewarded for choosing stimuli from one class over those from another (*A1* > *B1*). Thus trained, the subject generalized her knowledge so that when presented with any other *AB* stimulus pair, she always chose *A*. Speaking conservatively, these results only tell us that when presented with certain stimuli and rewarded for following a particular rule with a subset, a sea lion will generalize the rule and apply it to all the other members of that subset. The experiment does not tell us whether, in the absence of training and reward, the sea lion would naturally recognize this particular rule, or if she did recognize it, whether she would apply it generally beyond her immediate experience.

The distinction between learning that is rewarded in the laboratory and learning that occurs in the wild is important, because any intervention by humans that selectively rewards one kind of learning over another potentially distorts an animal’s natural method of acquiring and storing information. For example, pigeons trained to

match-to-sample with just a few stimuli are not able to transfer their behavior to novel stimuli, although monkeys and chimpanzees do so easily. However, pigeons do learn to match similar stimuli if they are trained with hundreds of exemplars over hundreds of trials. Apparently, although pigeons can acquire the abstract concept same-different, they seem predisposed to attend to absolute stimulus properties and to form item-specific associations (Wright et al. 1988; see also Wasserman et al. 1995; Shettleworth 1998). Extensive training by humans, therefore, changes the ways in which pigeons classify stimuli.

Similarly, Tomasello and colleagues compared the performance of chimpanzees raised by humans (but without language training), chimpanzees raised by their own mothers, and 2-year-old children. Human-reared chimpanzees showed more imitation (Tomasello et al. 1993), more joint attention, and were more likely to use gestures to direct a demonstrator’s attention (Carpenter et al. 1995) than chimpanzees raised by their own mothers. In another study, chimpanzees that had been trained to use tokens as symbols were able to solve match-to-sample tasks that required them to judge relations between relations. Naive chimpanzees could perceive these relations, but their knowledge seemed to remain tacit (Premack 1983; Thompson and Oden 1995). Mere exposure to humans, therefore, alters chimpanzees’ problem-solving skills.

Finally, consider the magnitude of the problem. In Schusterman’s and Kastak’s experiment, Rio learned a total of 180 dyadic (two-item) comparisons. This is roughly equivalent to the number of different dyadic comparisons—but not the number of triads—that confront a monkey in a group of 14 individuals. Most primates, however, live in much larger groups. In a group of 80 animals, each individual confronts 3160 different dyadic combinations and 82,160 different triadic combinations. In other words, free-ranging monkeys and apes face problems in learning and memory that are not just quantita-

tively but also qualitatively different from those presented in the typical laboratory experiment (Seyfarth and Cheney 2001).

What might constitute an adaptive solution to the social demands placed on monkeys? When asked to remember long strings of items, humans learn the string faster and remember it better if some kind of “rule” allows them to group items into “chunks” (Miller 1956; Tulving 1962). Similarly, when asked to remember the location of specific food types in a radial maze, rats act as if they have organized locations into groups according to the food type they contain (Dallal and Meck 1990; Macuda and Roberts 1995). Faced with the problem of remembering a large complex dataset, then, both humans and rats are predisposed to search for statistical regularities in the data (Seyfarth and Cheney 2001). They do so naturally and without reinforcement. Why should monkeys be any different?

In our current research we are testing the hypothesis that baboons organize knowledge about their social companions into a two-level, nested hierarchy based on matrilineal kinship and rank. Given that baboons respond strongly to evidence of a rank reversal between two individuals, we are using field playback experiments to test whether the subjects’ responses are stronger if the purported rank reversal involves two adjacently ranked individuals in different matrilineal lines compared with two adjacently ranked individuals in the same matriline (Seyfarth and Cheney in press).

Conclusion

To survive and reproduce, a monkey must be able to predict the behavior of others. In non-human primate groups, where alliances are common, prediction demands that a monkey learn and remember all of its opponents’ dyadic and triadic relations. The task is similar to the problems faced by humans and rats in memory experiments. In response to these pressures, we

suggest that nonhuman primates are innately predisposed to group other individuals into hierarchical classes, both for ease of recall and to facilitate predictions of behavior. The formation of hierarchical classes is an adaptive mental strategy, shaped by natural selection.

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