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Rhesus Macaques (*Macaca mulatta*) Categorize Unknown Conspecifics According to Their Dominance Relations

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The authors trained 3 adult male rhesus macaques (*Macaca mulatta*) to categorize pairs of unknown conspecifics presented in a video according to the dominance status of the videotaped monkeys. The subjects were trained to choose the dominant monkey for a category of films (e.g., films showing 1 monkey chasing another); then, new films were presented involving different conspecifics, and the monkeys' first responses to this new category of behavior (e.g., monkeys fighting) were taken as evidence of transfer. Two subjects were able to generalize categorical judgments of dominance to new films involving new behaviors. These findings seem to indicate that monkeys can use abstract social concepts and are aware of the social relationships within their group.

Most primates, including humans, live in social groups in which complex networks of kinship or affiliation, struggles for dominance, and shifting alliances are commonly observed. Behaviors observed in monkeys and apes (agonistic and dominance relationships not only between individuals but also between matrilines, opportunistic alliances, etc.) appear to be very similar to complex behaviors existing in humans (Cheney & Seyfarth, 1990). But, are monkeys and apes really conscious of the social complexity of their group and of what they are doing to manipulate conspecifics' behaviors? Can we find, as claimed by Byrne and Whiten (1988), a "Machiavellian intelligence" in animals other than ourselves?

Researchers suggest that the most important cognitive problems encountered by primates belong to the social area and that it is in response to the complexity of their social environment that cognitive processes have been developed in primates, including the human species (Byrne & Whiten, 1988; Humphrey, 1976; Jolly, 1966; Whiten & Byrne, 1997). This hypothesis is often called *social brain hypothesis* or *Machiavellian intelligence hypothesis*. The study of social cognition in apes and monkeys could thus lead to a better understanding of the evolution of human intelligence. As emphasized by Zayan and Vauclair (1998), however, to date, social categorization has been neglected by research on comparative cognition.

The literature indicates that primates can categorize various animal species presented on slides (Schrier, Angarella, & Povar, 1984; Swartz, 1983; Yoshikubo, 1985) or different pictures of the same individual (Bruce, 1982; Rosenfeld & van Hoesen, 1979). A particularly interesting experiment shows that monkeys are able to recognize the identity between photographs and the real conspecifics that are represented (Dasser, 1987a). Macaques are able to associate various pictures of a familiar conspecific's face with various pictures of its body. However, the subjects fail when the presented monkey is unknown.

Experiments about the categories of relations between individual nonhuman primates are much more rare. Some observations show that in various species monkeys or apes seem to know other conspecifics' social relations. For example, when vervet monkeys are played screams of free-ranging juveniles from their groups, the monkeys look at the juveniles' mothers, even without any apparent clue from the mothers (Cheney & Seyfarth, 1980). Another set of observations that suggests an understanding of third-party relationships concerns redirected aggression, in which monkeys that have been aggressed retaliate against the aggressor's affiliates (Aureli & van Schaik, 1991; Judge, 1982). Even the victim's kin are more likely to attack the aggressor's kin after an aggression (Aureli, Cozzolino, Cordischi, & Scucchi, 1992; Cheney & Seyfarth, 1986, 1989). Dominant females are more likely to supplant their subordinate partners following playbacks of sequences that mimicked a dispute between their relatives (Cheney & Seyfarth, 1999).

The dominance relations also seem to be perceived by nonhuman primates. For example, when baboons were played causally inconsistent sequences (in which a lower ranking female apparently grunts to a higher ranking female and the latter female apparently responds with fear barks), in 71% of the trials they looked at the speaker longer than when they were played causally consistent sequences (Cheney, Seyfarth, & Silk, 1995). Silk (1999) showed that male bonnet macaques involved in a conflict preferentially ask the support of males whose dominance rank is not only higher than theirs but also higher than their opponent's. Another observation deals with the high frequency of the inhibition of female chimpanzees' vocalizations when they mate with young males to avoid alerting the dominant male (Hauser, 1990).

These observations probably indicate that monkeys are able to understand third-party relationships concerning dominance rank. However, the mechanism used to classify relations is not well understood. In some cases, nonhuman primates may simply adjust their behavior according to past experiences rather than on the

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basis of perceived relations per se. For example, the inhibition by female chimpanzees of their vocalizations during mating with subordinate males could mean simply that the females learned that the dominant male would punish them if they vocalize when mating with other males. A laboratory approach to the study of social categorization can add to what is already known from field studies. In an experimental study of categorization, it is possible to choose the categories and the responses wanted from the subject. The subject's experience with the stimuli is also controlled; thus, in the current study, we used as stimuli conspecifics unknown to the subjects being tested.

The concept of mother–child affiliation in monkeys was tested by Dasser (1988b). In her experiment, 2 female long-tailed macaques were tested: one with a two-choice discrimination procedure (choice between pictures of mother–offspring pairs vs. pictures of pairs of unrelated individuals) and the other with a simultaneous matching-to-sample procedure (the sample being a slide of a mother, the positive alternative a slide of her offspring, and the negative alternative another individual). All the stimuli presented were groupmates of the subjects. Monkeys' performances were correct in 100% of the simultaneous discrimination trials and 90% of the simultaneous matching-to-sample trials. The only study involving an experimental categorization of the dominance relationship was also conducted by Dasser (1987b; quoted in Vauclair, 1996). In this experiment, a female long-tailed macaque was trained to choose the dominant monkey when a pair of slides showing members of her group was presented. The pictures of 3 group members were presented during the training, and then, the female was tested with pictures of other monkeys. The monkey consistently chose (in 82% of the trials) the subordinate monkey. Even though the results differ from chance, they are difficult to interpret because the subject chose subordinate monkeys despite being rewarded for choosing the dominant.

In our experiments, we tried to answer the following question: Are monkeys able to use the social concept of dominance to infer the relationship between unknown conspecifics? This was accomplished by training rhesus macaques to categorize 2 unknown conspecifics presented on a video according to their dominance status. This procedure was designed to test monkeys' capacities to use the dominance relation from social cues controlled by the experimenter.

Method

Subjects

Three male rhesus macaques (*Macaca mulatta*) were tested in this study: Baker, Willy, and Hank. The monkeys were born in captivity; they ranged in age from 13 to 19 years. They were treated in accordance with federal and university guidelines for the care of research animals. Each monkey was tested in individual 91 cm wide × 76 cm deep × 137 cm tall home cages with continuous visual and auditory contact with at least 1 conspecific. Compatible pairs of male monkeys were allowed to groom one another through the mesh of their cages. For approximately 2 weeks every 2 months, these compatible dyads were housed together in a large (5.0 m wide × 4.0 m deep × 2.5 m tall) social cage with access to a large (30.0 m wide × 15.0 m deep × 3.0 m tall) outdoor play yard. Baker and Willy were housed together; Baker was the dominant of the pair. Hank was housed with another macaque and was the subordinate of the pair. During testing, the monkeys had continuous access to a computerized test system (described below), to water, and, by means of task performance, to food. No monkey was deprived of food or reduced in body weight for purposes of testing. The 97-mg fruit-flavored chow pellets that could be obtained at any time by means of computer-task performances were augmented each day with chow, fruit, and vegetables. Rooms were maintained at 68–75 °F.

Apparatus

The monkeys were tested with the Language Research Center's (Department of Psychology, Georgia State University) computerized test system (Rumbaugh, Richardson, Washburn, Savage-Rumbaugh, & Hopkins, 1989). Each subject reached through the mesh of his home cage to respond to computer-generated stimuli by manipulating a standard, analog joystick. Movements of the joystick produced movements of a cursor on the computer screen in a direction isomorphic to the angle of joystick displacement. Bringing this cursor into contact with another computer-generated stimulus was recorded as a response. Correct responses were automatically reinforced with food pellets. Incorrect responses were followed by a 10-s time-out.

Films

Films were made by videotaping monkeys living in social groups of 50–150 individuals. These films were then screened for examples of eight behavioral categories (see Table 1). Useful segments of film (e.g., showing a dominant monkey chasing a subordinate) were digitized into 5-s clips. The films' format (they were very short and the monkeys shown were

Table 1
Films Presented to the Monkeys

Behavior category	Description	Number of different films presented
1. Chase	The dominant monkey chases the subordinate.	100
2. Avoidance	The subordinate monkey avoids the dominant's approach.	40
3. Presentation	The subordinate monkey presents its hindquarters toward the dominant.	20
4. Attack	The dominant monkey quickly attacks the subordinate.	10
5. Mounting	The dominant monkey mounts the subordinate.	10
6. Fight	The dominant monkey bites the subordinate while the subordinate is struggling to flee.	15
7. Bared-teeth display	The subordinate monkey looks mainly toward the dominant with a bared-teeth display and screams.	5
8. Food priority	The dominant monkey is eating while the subordinate is looking at it, not eating itself.	5

small and moving) as well as the great number of monkeys filmed made it highly unlikely that any of the specific monkeys presented could be recognized. Nevertheless, a new group of monkeys was filmed for each new category of behavior. As can be seen in Table 1, multiple examples of each behavioral category were obtained by this method, although the number of clips was relatively small for some categories.

Procedure

At the beginning of each trial, the monkey indicated that he was ready by bringing the cursor into contact with a start button (a pink square presented in the center of the screen). Then, a 5-s color digitized video was presented on the computer monitor, along with the sounds (monkeys vocalizations, etc.) of the video. The film showed 2 unknown rhesus macaques interacting with each other in a way allowing the observer to infer the dominance hierarchy between the 2 monkeys. At the end of the film, the last still frame was presented and the monkey was allowed to bring the cursor into contact with the image of one of the 2 stimulus monkeys. In training conditions, the subjects were rewarded for choosing the dominant monkey in each pair. The subjects were first trained with a set of five films in an order randomized for each subject. When they attained an accuracy level greater than 80% for each of those films, new sets of five films were presented and the monkeys were trained again. Thus, each new set of films was used as a novel test stimulus (the responses to the first presentation of each film were recorded) and as training stimuli (the films were subsequently presented again until criterion was attained). Trials with new films were randomly interspersed among trials involving familiar films. This was done to present the monkeys with a great variety of films and behaviors to encourage them to use a general concept of dominance instead of only learning the correct answer by rote for each film or category of behavior (which would have been easier to do with only the set of five new films presented in a session).

The eight behavior categories were presented in the same order (see Table 1) to each of the monkeys. A new behavior category was presented only when a monkey was able to respond correctly to the films showing the preceding category. Willy saw only the films showing the first behavior (chase), Baker saw the first seven behaviors, and Hank saw all eight behaviors. For Behavior Categories 1 and 2, only the first response to each new film was considered to assess transfer. For Behavior Categories 3–8, to obtain statistically interpretable data (because of the smaller number of available films in each category), we rewarded the monkeys for the first 10 responses for each new film presented (even if incorrect), and then, we trained the monkeys with the usual procedure (being rewarded only when correct). Only the first 10 responses to each new film (obtained under the always-rewarded procedure) were considered to assess transfer.

Results

Can a Monkey Categorize the Dominant Subject Across Different Films Presenting the Same Behavior?

The 3 monkeys were each shown 100 different films, all of which involved different individuals exhibiting in various ways the same category of behavior (chase). Willy, although able to memorize the correct responses to films already presented, always responded at chance level to the first presentation of new films. Baker and Hank also memorized the correct responses to films already presented, but they showed better-than-chance transfer to new films. For the last 25 films, Baker's first responses to new films were correct on 88% of the trials, $\chi^2(1, N = 25) = 14.4, p < .001$ (see Figure 1), and Hank's first responses to new films were correct on 76% of the trials, $\chi^2(1, N = 25) = 6.8, p < .01$ (see Figure 1).

Can a Monkey Categorize the Dominant Subject Across Films Showing Different Behaviors?

Willy was not tested in this phase because of his failure to generalize to new within-category films in the first phase. Baker responded at chance level for the first set of films exhibiting a second behavior (avoidance; see Figure 2). He demonstrated transfer performances for the subsequent sets of the same category of films: For the 30 other avoidance films, Baker's responses to new films were correct on 77% of the trials, $\chi^2(1, N = 30) = 8.5, p < .01$. The same pattern of response was found for the mounting films (see Figure 3): Responses were at chance for the first set, then above chance for the second one, $\chi^2(1, N = 50) = 8.5, p < .01$. In contrast, Baker's responses to three of the new behaviors were significantly better than chance from the very first presentation of the new films: presentation, $\chi^2(1, N = 50) = 3.9, p < .05$; fight, $\chi^2(1, N = 50) = 20.5, p < .001$; and bared-teeth display,

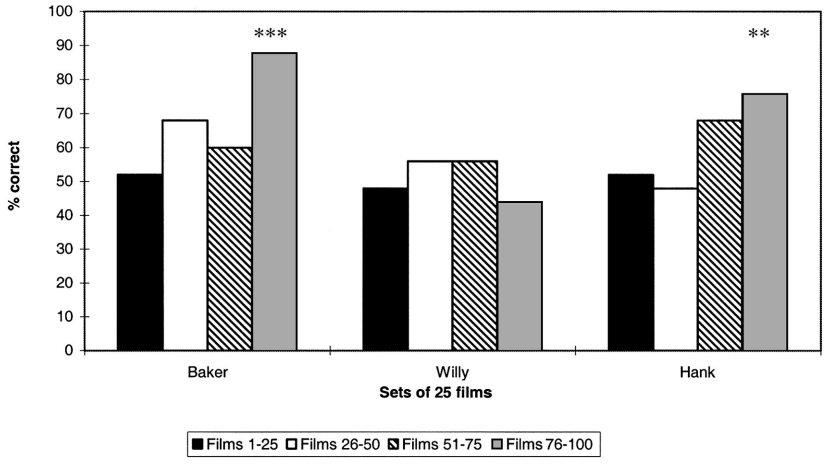

Figure 1. Monkeys' performances with the first category of films: chase. Only the answers to the first presentations of each film are taken into account. $^{**}p < .01$. $^{***}p < .001$.

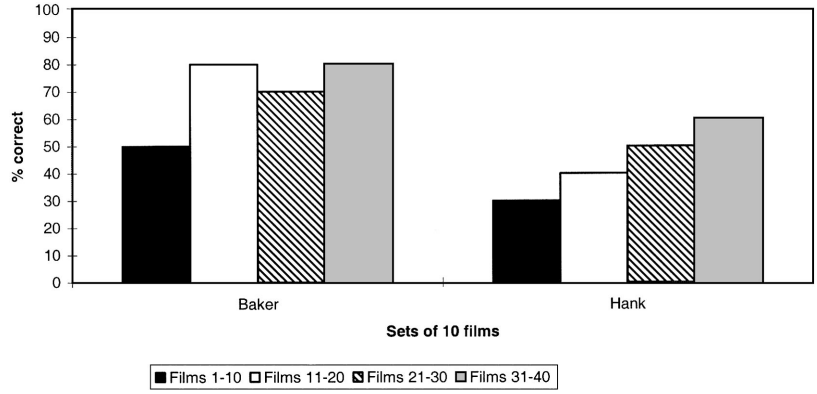

Figure 2. Monkeys' performances with the second category of films: avoidance. Only the answers to the first presentations of each film are taken into account.

$\chi^2(1, N = 50) = 13.5, p < .001$. No transfer was found for the attack films.

Hank responded at chance level for all sets of the avoidance and mount films. He responded at chance level to the first sets of the presentation and attack films and then demonstrated transfer performances for the subsequent sets of the same category of films: Hank's performances were correct for the last set of presentation films, $\chi^2(1, N = 50) = 3.9, p < .05$, and for the last set of attack films, $\chi^2(1, N = 50) = 8.0, p < .01$. Hank's responses to the three last behaviors were significantly better than chance from the very first presentation of the new films belonging to the categories fight, $\chi^2(1, N = 50) = 74.0, p < .001$; bared-teeth display, $\chi^2(1, N = 50) = 8.0, p < .01$; and food priority, $\chi^2(1, N = 50) = 3.9, p < .05$.

Discussion

The results of this study demonstrate that monkeys can categorize conspecifics according to their dominance relations. One of the rhesus macaques tested, Willy, responded at chance level to the first presentation of new films, but the 2 others were able to generalize categorical judgments of dominance not only to new films belonging to the category they had been trained with (for example, choosing the dominant individual in a film showing a monkey chasing another after being trained with films involving chasing behaviors) but also to new films involving new behaviors (for example, they chose the dominant monkeys on films exhibiting the fight behavior without having been trained beforehand with films showing this kind of behavior). Specifically, Baker chose the dominant monkeys on films exhibiting the presentation, fight, and bared-teeth display behaviors and Hank chose the dominant monkeys on films exhibiting the fight, bared-teeth display, and food priority behaviors without having been trained with films showing any of those of behaviors. The possibility that our subjects could use ways other than the behaviors to categorize their conspecifics is highly unlikely: Because of the matrilineal hierarchy, the dominant monkey could be younger and smaller than the subordinate. Thus, the dominant monkey was not systematically larger, older, or heavier than the subordinate, and there were not more errors when the dominant monkey was not larger, older, or heavier than the subordinate. We did not see any other distinct sign, such as erect fur, that would allow the observer to discriminate the monkeys presented without taking into account their behavior. The

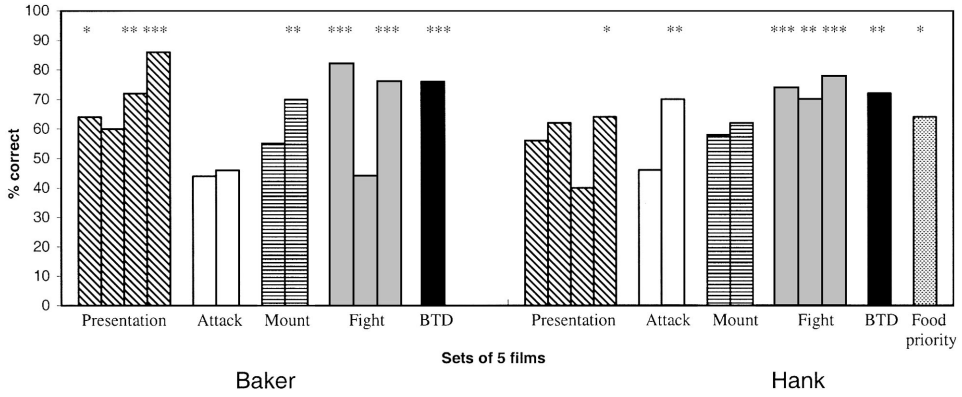

Figure 3. Monkeys' performances with the categories of films subsequent to chase and avoidance. Only the answers to the first 10 presentations of each film (under an always-rewarded procedure) are taken into account. BTD = bared-teeth display. $*p < .05$. $**p < .01$. $***p < .001$.

subordinate as well as the dominant monkey could move first, and although vocalizations recorded during each film were played, this could not help the subjects to categorize the individuals because the vocalizations were, unlike in real life, played by a speaker and thus not coming from one or the other of the monkeys.

The poor performances observed for Willy could be due to difficulty in recognizing the pictures presented. Although pictures are often presented in place of real objects in studies of categorization, there is often no proof that the subjects do really interpret the 2-D stimuli as the 3-D objects they represent. Many studies indicate that monkeys can have trouble recognizing pictures or films, especially when they are not accustomed to seeing 2-D pictures (Bovet & Vauclair, 2000). Among our 3 subjects, only Baker and Hank had seen videos before this experiment. This could possibly explain their better performances. Another potential problem is the poverty of the social life of our subjects. The monkeys were singly housed (but with visual and auditory access to another conspecific) about three quarters of the time and housed in dyads the remaining time. This precluded the possibility for our subjects to observe interactions between 2 other monkeys. They had, however, some experience of social life when infants and juveniles, and they had a hierarchical relation with their cagemate, which allowed them to know what it is like to be a subordinate (for Willy and Hank) or a dominant (for Baker).

Baker failed to categorize the subjects belonging to the first films of the avoidance, attack, and mounting behaviors, and Hank failed to categorize the subjects belonging to the first films of the presentation, avoidance, attack, and mounting behaviors. For the avoidance films, this failure could be because it was only the second category of behavior presented. Thus, it is possible that at that time Baker and Hank had not yet understood that they were supposed to class the monkeys presented according to their rank (they only understood at this point that they had to choose the monkey chasing the other). The same explanation can be suggested for Hank's failure with the presentation films: He was not yet using a dominance concept to categorize the subjects presented. For the attack and mounting films, failure could come from the kind of behaviors used. Although mounting behavior is often considered as a dominance indicator in rhesus monkeys (Wickler, 1967), other observations indicate that in this species mounting can be bidirectional and is commonly performed by subordinates (Reinhardt, Reinhardt, Bercovitch, & Goy, 1986). Subordinates also sometimes attack their dominants (in defense of themselves or their kin, for example). Therefore, those behaviors may not be reliable indicators of the dominance rank, which could explain the failure of Baker and Hank to use them at their first presentations to categorize the monkeys presented. Thus, for those films that may not have been clearly related to a dominance concept, the monkeys could have learned after the training what it was that we wanted them to do (i.e., choose the monkey attacking the other or choose the monkey mounting the other), but they were unable to answer correctly on the first presentation of the novel films.

Our monkeys' performances are less impressive then those observed by Dasser (1988b) in her experiment of mother–child concept. This may be a result of the quality of the films used. The monkeys may have had some trouble seeing what was going on in some films because of various characteristics of the films (size of the scenes, quickness of the movements, out-of-focus monkeys, etc.). Moreover, with each film lasting only 5 s and the relevant behavior often lasting for less than that, the monkeys could have been wrong on some trials because of attention failures: They sometimes did not attend to the whole film and thus missed the relevant behavior. In contrast, Dasser (1988b) showed still pictures of known groupmates to her subjects. The difference in performance between our study and the investigation by Dasser (1988b) could also reflect the concept of interest. When Dasser (1988a) trained a monkey to discriminate sibling pairs versus nonsibling pairs, the subjects' responses were correct for only 70% of the pairs. A dominance relationship is less stable and may be more abstract than a kin relationship. Indeed, when Dasser (1987b) tried to have a monkey attend to the dominance relationship between 2 groupmates, that subject tended to choose the subordinate monkey after being trained to choose the dominant. Our findings are more conclusive because Baker and Hank, contrary to Dasser's (1987b) subject, responded in the intended direction. Furthermore, our monkeys were able to infer the dominance relationship between 2 unknown conspecifics, whereas in Dasser's experiments the subjects were categorizing slides representing its group members. This gives a confirmation to the hypothesis of field researchers (Cheney & Seyfarth, 1990) who suggested that monkeys and apes could be aware of other conspecifics' relations.

We agree with de Waal (1989) that there is value and promise in examining the insights monkeys may have into their social networks, and we think our experiment brings some more validity to this hypothesis of monkeys having a rich knowledge of their social world. Our results are indicative that rhesus macaques could be able to infer the dominance relationship between unknown conspecifics, even with conspecifics presented only in a short video sequence. Thus, in agreement with the Machiavellian intelligence hypothesis, monkeys seem to be able to use concepts to order social relationships into types. As emphasized by Seyfarth and Cheney (2002), monkeys may be predisposed to group other individuals into hierarchical classes, both for ease of recall and to facilitate predictions of behavior. The ability to use concepts like dominance would make the monkeys' knowledge less constrained by particular stimuli, more general, and more abstract. This would enable them to construct cognitive categories of their groupmates' relationships and thus to make predictions about what could happen in a given circumstance (Tomasello & Call, 1997). We think that, as expressed by Byrne and Whiten (1988), social intelligence is a crucial key to understanding the problem of primate and human intelligence. The knowledge of other individuals' relationships can be useful to manipulate conspecifics' behaviors. Thus, the ability to deduce and to use concepts and abstract relations may exist in primates because of the advantage given to individuals who are able to understand other individuals' relationships.

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