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Learning by observation in rhesus monkeys

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Abstract

Habit memory provides us with a vast repertoire of learned rules, including stimulus-reward associations, that ensures fast and adapted decision making in daily life. Because we share this ability with monkeys, lesion and recording studies in rhesus macaques have played a key role in understanding the neural bases of individual trial-and-error habit learning. Humans, however, can learn new rules at a lower cost via observation of conspecifics. The neural properties underlying this more ecological form of habit learning remain unexplored, and it is unclear whether the rhesus macaque can be a useful model in this endeavor. We addressed this issue by testing four monkeys from the same social group in their usual semi-natural habitat using a well-established marker of habit memory, concurrent discrimination learning. Each monkey learned 24 lists of 10 object-reward associations each. For one list out of two, monkeys could observe the testing session of another member of the group prior to being tested with the same list themselves. Learning was faster for these lists than for those learned solely by trial-and-error. Errors to criterion (9/10 correct responses) were reduced by 39%, and faultless performance could be achieved for up to 5 of the 10 pairs. These data demonstrate that rhesus macaques spontaneously observe a conspecific learning new stimulus-reward associations, and substantially benefit from this observation. They ascertain that the neural underpinnings of socially-mediated forms of habit learning can be explored using the powerful tools of monkey research, including neurophysiological recordings.

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1. Introduction

From morning drives in rush-hour traffic to the selection of a restaurant for a family dinner, daily life entails an endless stream of minor decisions to make. To face this challenge, habit memory (Mishkin, Malamut, & Bachevalier, 1984) provides us with a vast repertoire of learned rules based on arbitrary associations between a stimulus and a movement (e.g. slow down when tail lights of the preceding car turn red) or a stimulus and a reward (between e.g. a big yellow M and a hamburger). Because we share this remarkable capacity with macaque monkeys, lesion and recording studies in macaques have played a key role in understanding the neural bases of individual habit learning. Together with lesion and imaging studies in humans, they have revealed the importance of the basal ganglia for the formation of new habits and the execution of acquired ones (Hadj-Bouziane, Meunier, & Boussaoud, 2003; Yin & Knowlton, 2006). Humans and macaques, however, are both social species and thus have the possibility to acquire knowledge at a lower cost via observation of conspecifics. The neural processes underlying the social transmission of habits are unknown, and whether the rhesus macaque can be a useful model in this new endeavor is uncertain.

Socially-mediated learning in primates was brought to the forefront of neuroscience research about 10 years ago by the discovery of mirror neurons in the macaque ventral premotor cortex, which fire during both execution and observation of goal-directed motor acts (Gallese, Keysers, & Rizzolatti, 2004; Rizzolatti & Craighero, 2004). Since then, behavior research has focused almost exclusively on...
solving the discrepancy between this discovery and the long held view that monkeys are poor imitators (Visalberghi & Fragaszy, 2002). Although controversy remains, this recent reevaluation of monkeys’ social skills has now provided evidence that macaques (1) have some understanding about what others see (Flombaum & Santos, 2005) or hear (Lyons, Santos, & Keil, 2006), a crucial skill for social learning, and (2) possess at least some ability to copy humans’ motor acts, in both adulthood (Kumashiro et al., 2003) and early infancy (Ferrari et al., 2006). By contrast, whether or not macaques can acquire new abstract rules, rather than motor acts, through observation of a conspecific remains virtually unexplored. Only two studies have tackled this issue over the last 37 years, an early one by Myers (1970), and a recent one by Subiaul, Cantlon, Holloway, and Terrace (2004). Both indicated that observation of an expert conspecific hastens subsequent individual learning of new complex rules in food-deprived, sophisticated laboratory animals. Here, we evaluate whether this skill truly belongs to the natural repertoire of macaques. We tested non-deprived naïve rhesus monkeys in their semi-natural social habitat using a well-established habit memory marker, concurrent discrimination learning, which is based on simple object-reward associations (Bachevalier & Mishkin, 1984; Buffalo, Stefanacci, Squire, & Zola, 1998; Fernandez-Ruiz, Wang, Aigner, & Mishkin, 2001). The animals spontaneously observed a non-expert conspecific, and did later benefit from this observation, thereby confirming the validity of the rhesus monkey as an animal model for brain research on social habit learning.

2. Methods

One of the social groups of the laboratory breeding colony participated in the study. It comprised five 2–4-year-old rhesus macaques (Macaca mulatta), three males: Mars, Billy, and Agilhas, and two females: Tanya and Lilou. They lived in a large enclosure comprising two areas, one indoor and one outdoor. Testing took place in the outdoor area which possessed a L-shaped tunnel made mostly of metal bars and equipped with three guillotine doors, one at each end and one in the middle. During a typical testing session (Fig. 1a), two animals were kept in the tunnel, separated by the middle guillotine door, in vocal contact with the rest of the troop which was confined into the indoor area. The experimenter sat on the floor in front of one of the two monkeys (the model), using a wooden tray equipped with two food wells to present pairs of objects, within view, but out of reach of the other monkey (the observer).

A pool of 540 “junk” objects (e.g. metal cans, cardboard boxes, plastic toys), varying in size, color, and texture, but all emotionally neutral (i.e. excluding items that macaques typically find attractive such as food or aversive such as dolls with staring eyes) were used to create 27 lists comprising 10 easily discriminable pairs of objects each. For each pair, only one object, always the same, concealed a treat (a chocolate candy or cereal puff, both items being unknown to the monkeys prior to the experiment). A new list was selected for each testing session and administered first to one monkey before testing was initiated; for each pair, when the animal’s attention was captured (i.e. when he/she tried to reach for the tray), the wells were uncovered to show the reward (without letting the animal retrieve it). The procedure was repeated twice as data from LeO sessions, in particular Tanya’s LeO scores, indicated that two list presentations were sufficient for observation of a conspecific to be beneficial. Testing during the control condition was conducted in presence of another member of the group, to maintain the same social context as for the T&E and LeO conditions.

The animals were not food deprived; they were fed after testing completion but received their normal food rations of fresh fruits and monkey chow. Nor were they trained to observe, the observer only occasionally withdrew the tray and repositioned the objects before allowing the animal eventually displaced the positive object. The left/right position of the positive object of each pair was unchanged on correction trials, but varied from one list presentation to the other according to a pseudorandom sequence to prevent motor imitation. The 10 pairs of the list were thus presented until the monkey reached 9/10 correct responses during a presentation or a maximum of 10 list presentations.

After the model reached the learning criterion (or, rarely, failed to within 10 presentations), the experimenter turned to the observer, and repeated the exact same procedure using the same list, correction procedure, and learning criterion. The animal which had served as a model remained in the tunnel during that time to maintain the same social context in all testing conditions. Testing partnership varied across sessions so that each individual interacted with at least two different peers across the experiment. Each monkey alternated between the model and observer roles over a total of 24 different lists. Thus, performance was alternatively measured under two conditions: when relying solely on individual learning (trial-and-error; T&E), versus after the animal had the opportunity to observe the learning session of another member of the troop (learning by observation; LeO). For Tanya, who was the first monkey to undergo testing, the procedure used was identical except that (1) she was free in the outdoor area, rather than restrained in the tunnel (Fig. 1b and c), and (2) she was provided with only two presentations of the list in the LeO condition, rather than a full learning session.

As learning was found to be faster for LeO lists, 3 additional lists were administered to determine whether the same benefit could be obtained without the mediation of a conspecific actually interacting with the objects and rewards. In this control condition, the experimenter presented a new list to the monkey before testing was initiated; for each pair, when the animal’s attention was captured (i.e. when she/he tried to reach for the tray), the wells were uncovered to show the reward (without letting the animal retrieve it). The procedure was repeated twice as data from LeO sessions, in particular Tanya’s LeO scores, indicated that two list presentations were sufficient for observation of a conspecific to be beneficial. Testing during the control condition was conducted in presence of another member of the group, to maintain the same social context as for the T&E and LeO conditions.

The animals were not food deprived; they were fed after testing completion but received their normal food rations of fresh fruits and monkey chow. Nor were they trained to observe, the observer only occasionally received a treat during the model’s testing. The experimental design was thus intentionally constructed to assess the animals’ spontaneous willingness to observe and benefit from another’s behavior, without any conditioning besides the task basic principle (displace only one object at a time). Lilou proved too impulsive to master the task. The other 4 monkeys completed the 12 T&E, 12 LeO, and 3 control lists. For each list, 4 scores were calculated: (1) the number of errors (i.e. correction trials) cumulated over the different list presentations necessary to reach the criterion of 9/10 correct responses (or, rarely, the failure limit of 10 presentations), (2) the number of list presentations to criterion, (3) the number of errors made during the first presentation of the list and (4) the number of pairs out of the 10 comprising each list for which the animal showed faultless performance, that is, responded correctly throughout all the presentations of the list.

3. Results

3.1. Behavior during observation

During the observation phase, two types of behavior emerged. Tanya, a poised female, and Agilhas, the bottom ranking male, spent long bouts of time sitting quietly and...
overtly monitoring the experimenter’s and model’s activities, whereas Mars and Billy, the respectively top and middle ranking males, seldom stop and stare. Rather, they merely glanced at the model while pacing in the tunnel. Common to all four monkeys, however, were occasional aggressive reactions to the sight of the model retrieving the reward, the restrained males displaying mouth threats and body lunges, while free Tanya actually went and hit the model through the tunnel bars.

3.2. Overall benefit from observation

All four animals gained information during observation that improved subsequent trial-and-error learning. This benefit was substantial, errors to criterion during the 12 LeO sessions were reduced by an average of 39% relative to the 12 T&E sessions (Fig. 2). A $4 \times 2$, monkey $\times$ learning condition ANOVA, with repeated measures for the second factor, confirmed the benefit brought to trial-and-error learning by previous observation of a conspecific (condition: $F_{1,44} = 25.04, p < 0.001$). The magnitude of this benefit did not differ across animals (monkey $\times$ condition interaction: $F_{3,44} = 0.18$, n.s.) despite their differences in terms of gender, social rank, attention abilities during observation, and individual scores during T&E sessions.
As illustrated in Fig. 3, observation also consistently decreased the number of list presentations necessary to reach criterion (means ± SEM: LeO, 4.6 ± 0.4; T&E, 6.1 ± 0.2; paired t-test, \( t = 5.7, p = 0.01 \)), as well as the numbers of errors committed during the very first presentation of each list (right panel). * Paired t-tests, \( p < 0.05 \).

3.3. Amount of information gained through observation

Faultless performance for a given pair can be achieved either by single-trial individual learning (the positive object being found by chance during the first list presentation and remembered throughout all subsequent presentations), or by using information acquired through observation. During T&E sessions, individual learning provided faultless performance for an average of 2.5/10 pairs (min: 1.8 for Agilhas; max: 3.1 for Billy). During LeO sessions, the number of errorless pairs significantly increased, reaching an average of 3.3/10 pairs (min: 2.6 for Agilhas; max: 4.2 for Billy; paired t-test, \( t = 5.4, p = 0.01 \)), indicating that at least 0.8/10 pair was acquired solely through observation during LeO sessions. When observation was especially efficient (i.e. when only the best four LeO sessions were considered for each animal), the number of errorless pairs raised up to an average of 5.0/10 pairs (min: 3.3 for Tanya; max: 7.0 for Billy; paired t-test, \( t = 3.6, p = 0.04 \)). Thus, at its best, observation provided the animals with faultless performance for twice as many associations (5/10) as typically achieved by individual learning alone (2.5/10).

3.4. Human versus monkey modeling

Performance over the three control lists was compared to that observed over the immediately preceding six experimental lists, that is, the last three T&E and the last three LeO lists (Fig. 4). Performance varied across the three conditions (condition: \( F_{2,16} = 9.6, \) Huynh-Feldt \( p = 0.002 \)) in all animals alike (monkey × condition interaction: \( F_{5,16} = 1.4, \) n.s.). Contrast analyses confirmed that scores for LeO lists were significantly better that those observed for both the T&E and control conditions (\( p = 0.01 \)), while the two latter conditions did not differ from each other. Display of the correct associations by the experimenter thus failed to reproduce the benefit brought by observation of a conspecific actually interacting with the objects and consuming the rewards. Rather, the control condition, during which all the animal’s attempts to retrieve the reward were thwarted, slightly hindered learning relative to the T&E condition.

4. Discussion

4.1. Observation can be sporadic in macaques

The present experimental design was constructed to assess macaques’ spontaneous willingness to observe and benefit from another’s learning. A stable social group was tested in its usual semi-natural surroundings, with minimal constraints and conditioning, and the animals were not trained to observe. The results show that all group members naturally observed when a conspecific was tested nearby, though they differed in the time spent overtly attending to the monkey model. Occasional glances were
sufficient for the two dominant males to glean useful information, whereas the female and the subordinate male did so via long bouts of overt monitoring. Pig-tailed macaques have been reported to pay less attention to a conspecific’s demonstration (of ways to open an artificial fruit) than chimpanzees and human children or adults (Custance, Prato-Previde, Spiezio, Rigamonti, & Poli, 2006; Rigamonti, Custance, Previde, & Spiezio, 2005). Our present observations corroborate the idea that attention during observation can be sporadic in macaques. They suggest, however, that some individuals (perhaps the most quiet ones) may nevertheless be dedicated observers. In addition, the outbursts of anger elicited by the monkey model in the present study suggest that competition over coveted food items (here, sugary items for which the group developed a strong liking over the experiment) could serve as an incentive to foster observation in macaques.

4.2. Converging evidence that macaques can learn new habits by observation

All four monkeys learned new lists of 10 object-reward associations faster after having observed a conspecific learning the same list than by trial-and-error learning alone. Errors to criterion during individual trial-and-error dropped by more than a third after observation (39%). The animals could show faultless performance for 5 out of the 10 associations of a list (up to 7/10 for Billy, our best learner), and at least half of this knowledge can safely be considered as acquired solely through observation. This clearcut benefit of observation stands in stark contrast with the negative or mitigated evidence often reported in monkey motor imitation studies (e.g. Custance et al., 2006; Rigamonti et al., 2005). Yet, it is in total agreement with the two studies that have used abstract rules rather than motor acts to explore social learning in macaques (Myers, 1970; Subiaul et al., 2004; see also Brosnan & de Waal, 2004 for similar positive results in capuchins). Myers (1970) reported that two males (one rhesus and one stump-tail) who had had the opportunity to observe a conspecific expertly execute complex reinforcement schedules subsequently performed better than control animals lacking the chance to observe. Subiaul et al. (2004) used a within-subject design similar to the present one in two rhesus males; each animal learned the ordinal position of four images faster after observing the other expertly execute the sequence than when they had to learn a new sequence solely by trial-and-error. The present data strengthen these earlier findings in two respects. First, they show that the capacity to benefit from observation to acquire new rules is not an artificial “human-enforced” skill specific to food-deprived laboratory macaques confronted with slowly learned complex tasks. It is naturally present in non-deprived naïve rhesus monkeys living in a semi-natural social context and faced with a task that they easily master. Second, this capacity is not restricted to subordinate males of social dyads (Myers, 1970) or single-housed males of unknown social status (Subiaul et al., 2004). Provided they have normal individual learning abilities, all members of a social group are likely to benefit from observation, whether male or female, dominant or subordinate, overt or covert observers, good or bad learners. These findings ascertain that, whatever their ability to copy specific motor acts might be, macaques can and do benefit from observation of a conspecific to acquire new cognitive rules.

4.3. The model competence: a factor to be explored

Another noteworthy originality of the present study is that the monkey model was acquiring new stimulus-reward associations rather than expertly executing previously learned ones. This choice was inspired by (1) human data suggesting that children learn more from the coping behavior of a novice peer than from the perfect mastery of an expert one (Schunk, 1987) and (2) animal data showing that birds, for example, faced with a discrimination problem learn more from conspecifics’ mistakes than successes (Templeton, 1998). The novice model could explain the apparently greater benefit obtained here compared to the gains described earlier in similar within-subject designs using expert models. In macaques, Subiaul et al. (2004) found a 24–26% increase in accuracy for only two of the four items of an ordinal sequence after 40 presentations of the sequence by an expert conspecific. In capuchins, Brosnan and de Waal (2004) reported a 20% increase in preference for the object of a pair worth a high-value reward after 10 presentations of the pair by an expert conspecific. By contrast, in the present study, 2–10 presentations of a list of 10 associations by a novice conspecific were sufficient to yield a 39% drop in the number of errors to criterion. Further studies are needed to formally compare the efficiency of novice versus expert models in monkeys, as well as to determine whether monkeys can ever reach perfection solely through observation. Meanwhile, available data already indicate that observation reliably results in modest to substantial performance improvement.

4.4. Mechanisms of knowledge transfer

Which mechanisms ensured knowledge transfer during observation? As in Subiaul et al.’s earlier study (2004), neither social facilitation (the potential benefit brought by the mere presence of a conspecific), nor motor imitation can account for the present findings. Monkeys were never tested in isolation and the positive object position varied pseudorandomly over the different list presentations, making learning of left/right movements irrelevant. The failure of our control condition to facilitate subsequent learning narrows the possibilities. In this condition, monkeys saw a human manipulating objects and rewards, whereas in the LeO condition they saw a conspecific manipulating the objects and consuming the rewards. A conspecific model is probably more appropriate than a heterospecific one to trigger social identification (Brosnan & de Waal,
2004) and, as noted above, competition over coveted food items may focus attention during observation. Both factors could thus contribute to the salience of positive objects, thereby ensuring knowledge transfer. A third factor that possibly contributed as well is novelty. Novelty has been suggested to be critical for social learning to occur in chimpanzees (Hirata & Morimura, 2000) and capuchins (Brosnan & de Waal, 2004). Likewise, the use of a new list of object pairs for each session may have maintained macaques' interest throughout the experiment even when the task became familiar.

5. Conclusion

It is beyond the scope of this paper to determine whether the facilitation of individual rule learning that follows observation should be considered as true imitation or not (see e.g. Byrne & Russon, 1998 for a theoretical review). The point here is that this facilitation naturally and reliably occurs in rhesus monkeys, thereby establishing the validity of this animal model for investigating the neural bases of learning by observation. Although social learning is at the core of the transmission of tradition and culture (Castro & Toro, 2004), how social variables influence the brain implementation of cognitive functions remains unknown. Do mirror-like properties, akin to those observed in the ventral premotor cortex for motor acts, also exist in the basal ganglia for abstract rules? The present behavioral data open the way for future recording studies addressing this question.

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