

Capuchin Monkeys Display Affiliation Toward Humans Who Imitate Them

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During social interactions, humans often unconsciously and unintentionally imitate the behaviors of others, which increases rapport, liking, and empathy between interaction partners. This effect is thought to be an evolutionary adaptation that facilitates group living and may be shared, therefore, with other primate species. Here we show that capuchin monkeys, a highly social primate species, prefer human imitators over non-imitators in a variety of ways: The monkeys look longer at imitators, spend more time in proximity to imitators, and choose to interact more frequently with imitators in a token exchange task. These results demonstrate that imitation can promote affiliation in nonhuman primates. Behavior matching that leads to prosocial behaviors toward others may have been one of the mechanisms at the basis of altruistic behavioral tendencies in capuchins and in other primates, including humans.

In everyday life, we often unintentionally take on the body postures of, make gestures that imitate, and exhibit mannerisms of our social interaction partners (1), a phenomenon that has been termed the “chameleon effect” (2). This form of imitation, which occurs completely unconsciously, can have profound effects on subsequent social interactions: The imitated person reports increases in shared rapport, liking, and feelings of empathy with the interaction partner (2) and is also more likely to display prosocial behaviors such as helping others, leaving more generous tips, or donating money to charity (3, 4). Imitation therefore increases affiliation, empathy, and rapport between individuals, and it undoubtedly plays an important role in maintaining harmonious relationships with others (5).

Being able to cultivate successful social relationships is likely to carry substantial adaptive value. Individuals with strong social bonds who receive support from others are thought to have an evolutionary advantage over those who are ostracized from a group (3, 5). Nonconscious imitation may therefore be an evolutionary adaptation that facilitates group living and may occur among other social primate species. Great apes and macaques share with us the capacity to recognize imitation (6–8), but it is presently unclear whether imitation may also facilitate positive social interactions in nonhuman primates. That is, do other primates show increased levels of affiliation toward an individual who displays behaviors similar to their own? We addressed this question by studying the effects of

imitation on the behavior of capuchin monkeys, a highly social and socially tolerant New World primate species. Observational and experimental evidence suggests that capuchins are easily influenced by others' behavior (9–11) and are thus likely to recognize when others display behaviors matching their own actions. Moreover, because capuchins are strongly bonded into social groups, they may share with humans this mechanism to facilitate social group living; namely, increasing affiliation toward those who display matching behaviors. We investigated whether capuchins recognize imitation and whether imitation positively affects capuchins' social interactions.

In experiment 1, we investigated whether capuchins differentiate between an experimenter imitating them and an experimenter performing contingent actions but not imitating them. Following the established research designs with infants (12, 13), two experimenters, each holding a small plastic ball, faced each monkey (Fig. 1). During the baseline phase, both experimenters performed actions that are commonly performed by capuchins (poking the ball with their fingers, mouthing the ball, and pounding the ball on a surface) (14). Analysis of visual preferences showed that monkeys did not discriminate between experimenters [mean, 36.23 s for the first experimenter and 40.05 s for the second experimenter, $t(10) = -0.81, P = 0.44$]. During the manipulation phase, monkeys were given an identical ball. One experimenter imitated the monkeys' ball-directed actions, whereas the other experimenter performed contingent but nonmatching actions (14). Monkeys looked longer at the imitator while they were manipulating the ball and hence while they were being imitated by the imitator [$t(10) = 2.23, P = 0.050$] (Fig. 2). Thus, capuchins are sensitive to the actions of others that match their own actions, and they prefer to look at imitating individuals.

Proximity to others is a reliable indicator of underlying affiliative relationships in capuchins and other primates (15). We therefore tested

whether capuchins show increased proximity to an imitator rather than a non-imitator. At the start of experiment 2, two experimenters faced each monkey for a 1-min period, one standing on the left side and one standing on the right side of a test cage. Monkeys could freely move within the three chambers of the test cage and choose whether to spend time in front of one of the experimenters or in a neutral middle position equidistant between experimenters (Fig. 1). During the first proximity measurement, monkeys spent similar amounts of time in front of both experimenters [41.2 and 36.0% of the trial; $t(9) = 0.65, P = 0.53$] (Fig. 3). As in experiment 1, monkeys were then given a small plastic ball, and one experimenter imitated the monkey's ball-directed actions while the other performed temporally contingent but structurally nonmatching actions. Monkeys looked longer at the imitator while manipulating the ball and hence while being imitated [$t(9) = 2.95, P = 0.016$] (Fig. 2). After the manipulation phase, imitator and non-imitator switched positions in front of the test cage, and for 1 min, monkeys could again choose whether to spend time in front of an experimenter or in the middle of the test cage equidistant between experimenters. Monkeys now spent significantly more time in front of the imitator than the non-imitator [mean imitator, 44.0%; mean non-imitator, 27.1% of the trial; $t(9) = 2.29, P = 0.048$] (Fig. 3).

One possible explanation for this effect might be that it is not imitation, per se, but rather it is the difference in looking time during the manipulation phase that led to the monkeys having greater familiarity with the imitator and thereby might have caused the shift in the monkeys' preference for the imitating experimenter. Alternatively, the imitator may have been perceived as being more attentive to the monkeys and therefore may have been preferred in the subsequent proximity test. To test whether attention alone may have caused the observed effect on social preference, in experiment 3 we first conducted a baseline proximity preference as in experiment 2. Two experimenters stood in front of the monkeys, one to the left and one to the right of the test cage, and for 1 min, monkeys could choose to spend time in front of an experimenter or in the middle of the test cage equidistant between experimenters. Monkeys spent similar amounts of time in front of both experimenters [36.9 and 32.0% of the trial; $t(10) = 0.74, P = 0.48$] (Fig. 3). Monkeys were then given a small plastic ball, and one experimenter faced and looked at the monkeys, whereas the other experimenter turned around and faced away from the monkeys. Both experimenters remained passive throughout the test phase and did not move while the monkeys manipulated the ball. Being sensitive to gaze (16), monkeys looked significantly longer at the experimenter facing them during the manipulation phase [$t(10) = 6.41, P < 0.001$] (Fig. 2). After the manipulation phase, the two experimenters switched places in

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front of the test cage, and monkeys could again choose for 1 min whether to spend time in front of one of the experimenters or in the middle of the test cage equidistant between experimenters. Unlike in experiment 2, monkeys now spent similar amounts of time in front of experimenters [mean looking at monkey, 37.8%; mean looking away from monkey, 27.4% of the trial; $t(10) = 1.56, P = 0.15$] (Fig. 3). Thus, it appears that it is the process of being imitated rather than simple familiarity that caused monkeys to increase proximity to the imitator in experiment 2.

To investigate whether imitation also affects social interactions, we tested the effects of imitation on monkeys' interactions with an imitator in a token exchange task. A token exchange by its very nature is an interaction between two partners, one providing a token and the other providing a food item (17). Several factors may influence a monkey's willingness to exchange tokens with an experimenter; for example, a monkey might refuse to exchange tokens with a person whom they fear [supporting online ma-

terial (SOM) text]. Therefore, a monkey's emotional reaction toward an experimenter may significantly affect a monkey's willingness to exchange tokens. All of our monkeys had previously been trained to exchange small metal or plastic tokens with human experimenters for food rewards. In experiment 4, monkeys could choose to exchange a token with one of two experimenters, both offering the same food reward (a small piece of marshmallow). During the first token exchange session, monkeys did not prefer either experimenter for their token exchanges [mean, 4.55 and 5.15 exchanges; $t(9) = -0.25, P = 0.81$] (Fig. 3). Immediately after this first token exchange session, we replicated experiment 1. During the baseline imitation phase, monkeys did not visually discriminate between the experimenters [mean, 37.25 and 40.19 s; $t(9) = -0.93, P = 0.37$]. During the experimental imitation manipulation, monkeys showed a visual preference for the imitator during imitated actions [$t(9) = 3.12, P = 0.012$] (Fig. 2). Finally, we conducted a second token exchange session,

in which monkeys could choose to exchange a token with either the imitator or the non-imitator, again receiving the same food reward from both experimenters. Monkeys now exchanged significantly more frequently with the imitator [mean imitator, 6.05; mean non-imitator, 4.95 exchanges; $t(9) = 2.30, P = 0.047$] (Fig. 3), indicating that being imitated increased the frequency of the monkeys' interactions with the imitator.

To confirm that, like the proximity measurements, the token exchanges were not merely facilitated by increased familiarity or perceived attentiveness of the imitator, we ran experiment 5 as a control study. At the start of experiment 5, monkeys could exchange tokens with one of two experimenters, who offered identical food rewards. As in experiment 4, monkeys initially did not prefer either experimenter [mean, 4.55 and 5.45 exchanges; $t(9) = -0.95, P = 0.37$] (Fig. 3). We then replicated the gaze control manipulation from experiment 3; that is, one experimenter faced and looked directly at the monkeys, whereas the other experimenter turned around and faced away from the monkeys, which led to monkeys looking significantly longer at the experimenter facing them [$t(9) = 3.51, P = 0.007$] (Fig. 2). A second token exchange session, which immediately followed the manipulation phase, revealed, however, that monkeys did not prefer to exchange tokens with the experimenter who had faced them during the manipulation phase [mean looking at monkey, 4.8; mean looking away from monkey, 5.2 exchanges; $t(9) = -0.49, P = 0.64$] (Fig. 3). Experiment 5 therefore confirms that it is the process of being imitated that led to increased interactions with the imitator.

These experimental results demonstrate that imitation significantly affects the behavior of capuchin monkeys: They look longer at imitators, spend more time in proximity to imitators, and prefer to interact with imitators in a token exchange task. As control experiments 3 and 5 show, these behavioral preferences cannot be solely explained by familiarity or the perceived attentiveness of the imitator. Thus, imitation positively affects subsequent social interactions not only in humans but also in capuchin monkeys.

Increased affiliation in human studies is observed after the matching of subtle gestures (2, 5) or synchronized movement between individuals (18), not the conspicuous imitation shown in the present study. Moreover, it is generally accepted that capuchins do not explicitly match actions in the precise and timed manner of the human imitator in the present study (9, 15, 19). How well do these effects, which were observed under controlled laboratory conditions, transfer to capuchins' natural group environment? Precise data on this phenomenon in group settings are clearly needed, but it is known that wild capuchin groups routinely synchronize their behavior; for example, for travel, feeding, and predator defense (15). It is possible that such group synchronization may provide a sufficient degree of behavioral matching to produce positive effects on

Fig. 1. Schematic of experimental setup in experiments 1 through 5. For proximity measures and token exchanges, monkeys had access to cages A through C. Monkeys were considered to be in proximity to an experimenter when they entered cage A or C. During the manipulation phases (imitation or gaze control), monkeys were restricted to cage B.

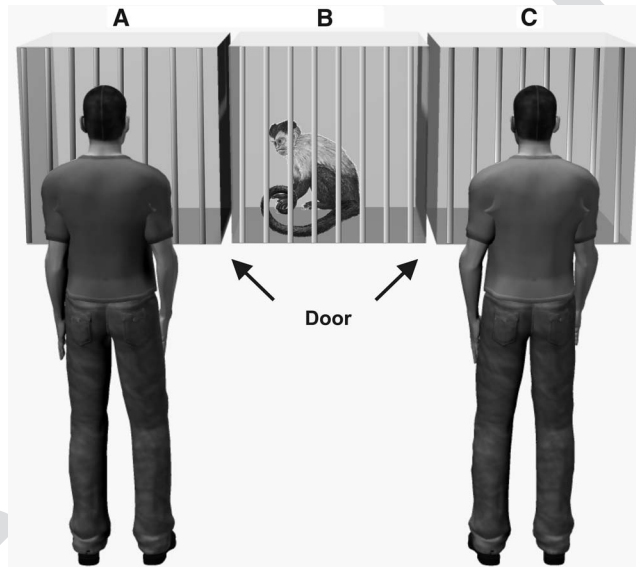


Fig. 2. Average looking time at experimenters while monkeys were manipulating the ball during manipulation phases (imitation or gaze control) in experiments 1 through 5. Gray bars represent the imitator/experimenter facing the monkey; white bars represent the non-imitator/experimenter facing away from the monkey. * $P = 0.05$, ** $P < 0.05$, two-tailed t tests [experiments 1 and 3, $n = 11$ trials; experiments 2, 4, and 5, $n = 10$ trials; see (14)]. Error bars represent SEM.

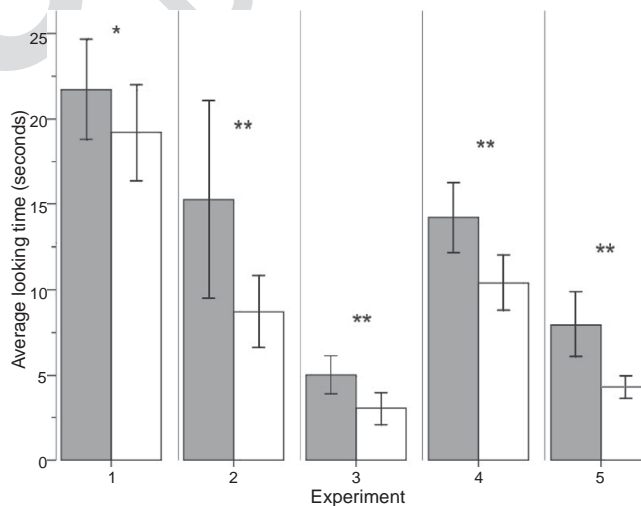
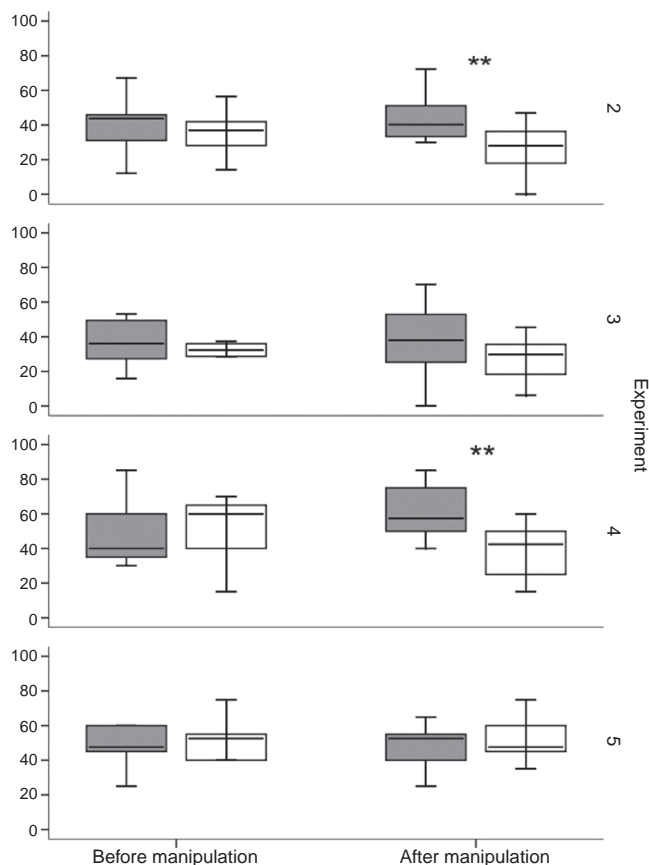


Fig. 3. Average behavioral preferences (proximity and token exchanges) for experimenters in experiments 2 through 5 before and after the manipulation phases (imitation and gaze control). Proximity measures in experiments 2 and 3 were converted into a percentage of the total phase duration. Token exchanges in experiments 4 and 5 were converted into a percentage of total exchanges (10 trials per phase = 100%). The top of the boxes represents the 75th percentile, the bottom of the boxes represents the 25th percentile, and the line in the middle represents the median. Gray boxes represent the imitator/experimenter facing the monkey; white boxes represent the non-imitator/experimenter facing away from the monkey. **** $P < 0.05$, two-tailed t tests.**



subsequent social interactions. Moreover, monkeys are unlikely to understand others' intentions to imitate them (SOM text) (8), which suggests that explicit and implicit matching of behaviors are likely to affect them in similar ways. Matching or synchronization of behaviors may therefore carry substantial adaptive value not only as a mechanism of social learning (20) but also through its effects on subsequent social interactions.

It has been argued that the link between behavior matching and increases in affiliation might have played an important role in human evolution by helping to maintain harmonious relationships between individuals (21). We propose that the same principle also holds for other group-living primates. Matching or coordination of behaviors may lead to higher levels of tolerance and

affiliation as well as decreases in aggressive behaviors, thereby increasing group cohesion. Behavior matching can therefore be regarded as a type of "social glue," helping to bind individuals together (21). The effects of behavior matching are not necessarily restricted to only two interaction partners, but may also lead to pro-social behaviors toward other individuals who were not directly involved in the social imitative exchange (3). An empathic connection resulting from behavior matching (2) may therefore extend to others in the social environment and promote altruistic behavioral tendencies in capuchins (22) and humans (3, 4).

References and Notes

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Materials and Methods

SOM Text

References and Notes

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