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ORIGINAL PAPER

Copying without rewards: socially influenced foraging decisions among brown capuchin monkeys

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Abstract An individual's foraging activity can be influenced by the choices made by nearby conspecifics. The interest shown in the location and characteristics of a feeding patch may depend on the feeding success of a conspecific there, a process that needs to be distinguished from choices guided by rewards to the observer itself. We investigated how rewards for both self and others influence the foraging choices of captive capuchin monkeys (*Cebus apella*). Thirteen adult capuchins observed familiar female conspecific models explore one of three opaque boxes under three conditions. In the first, there were no rewards available to either monkey; in the second, rewards were available to the model only; and in the third, both monkeys could retrieve a reward. Under all conditions, subjects more often explored the same box as the model than was expected by chance. Thus, without ever receiving a reward themselves or without seeing another receive rewards, subjects' searches were directed at the box explored by another monkey. The tendency to match the model's choice increased if the subject was rewarded. We compared these results to control conditions in which the model was either absent, or present but not allowed to demonstrate. Subjects' located the reward less often in control conditions, than in the experimental conditions. We conclude that extrinsic rewards, while helpful, are not required for partners to influence the foraging choices of capuchins, and that the unrewarded copying of foraging choices demonstrated here may provide the basis for additional social influences on learning.

Keywords Socially biased learning · Social learning · Stimulus enhancement · Reinforcement

Introduction

Among primates, an individual's foraging activity may be influenced by the feeding activities of nearby conspecifics. By watching older members of their social group, for example, infants and juveniles learn how to locate and process nutritious foods (Janson and van Schaik 1993). Adults, too, benefit from attending to the feeding behavior of other adults and may learn if a resource patch is profitable (Valone and Templeton 2002) or if foods are palatable or safe to eat (Snowdon and Boe 2003; Prescott et al. 2005; but see Visalberghi and Addessi 2003 for contrasting evidence). Indeed, observing others potentially yields a number of adaptive benefits, including also the time and/or energy saved by an individual during the acquisition of successful foraging strategies.

It has been argued that the benefits provided by the behavior of a social partner require that reinforcement must also take place at the individual level. It is therefore not surprising that nearly all previous studies of socially-biased learning have involved rewarded behavior (Caldwell and Whiten 2002). Yet, the role of reward in governing how behavior is acquired or maintained through the observation of others remains a contentious issue (Miklosi 1999). At present, there

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has been no focused effort to tease apart the various possibilities of how rewards affect the behaviors of observers in a social context. This may be due in part to the heavy focus of research on imitation and other complex learning mechanisms. But such complex copying is not required for observable changes to occur. Conspecifics also influence each other's foraging decisions by enhancing the relevance of objects (stimulus enhancement) or locations (local enhancement) in the environment (Nicol 1995; Fragaszy and Visalberghi 2001; Fragaszy and Visalberghi 2004). It is at this level of influence that our study is focused.

Observation of a conspecific successfully acquiring a reward may enhance the attention given to a modeled behavior or reward acquisition may act as a discriminating cue among aspects of the environment (Palameta and Lefebvre 1985). This theory, which we will call the *Vicarious Reinforcement Model* (VRM) suggests that the reward gained by a model acts as a motivational primer, i.e., an overt cue to the observer that the model's behavior is successful (Bandura 1977; Miklosi 1999). For example, individuals acquired a simple discrimination task only after having seen a conspecific obtain a reward from the same location on an earlier trial (Darby and Riopelle 1959, *Macaca mulatta*; Palameta and Lefebvre 1985, *Columbia livia*; Akins and Zentall 1998, *Coturnix japonica*).

In contrast to VRM, reinforcement-oriented theories predict that behaviors arise from social interactions only in concert with individual experience, in which successful trials are rewarded and other trials are not (Heyes et al. 1993). In other words, a socially acquired behavior must be effective, relative to other behavioral variants, in producing rewards for the observer; if not, the behavior will not be maintained (Galef 1992). This hypothesis, which we will call the *Reinforced Observational Learning Model* (ROLM), treats learning in a social context as a special case of individual learning, i.e., postulates the same dependence on extrinsic reinforcement that is part of operant conditioning paradigms of individual learning. ROLM acknowledges that social partners may affect the initial acquisition of a novel behavior, but predicts that in the absence of positive reinforcement for the observer, a recently acquired behavior would either extinguish or be replaced by an alternative method. For example, budgerigars (*Melopsittacus undulatus*) copied the method (using beak or feet) of a conspecific demonstrator to remove a cover from a small container with food, but only on the first two trials after observation (Galef et al. 1986). On subsequent trials, subjects no longer showed a preference for the demonstrated method over equally successful alternatives.

Alternatively, social influences on behavior may not depend on the acquisition of rewards by either models or observers, but rest on affiliative motivations (Bonnie and de Waal 2006; Matsuzawa et al. 2001). This idea, which de Waal (2001) formulated as the *Bonding- and Identification-based Observational Learning* (BIOL) model stresses the intrinsically rewarding quality of acting like others, especially those close to the subject, with whom the subject "identifies" (cf. de Waal 1998, 2007). The same idea underlies Matsuzawa et al.'s (2001) education by master-apprenticeship in which individuals observe specific related individuals (e.g., a juvenile's mother) for long periods before themselves attempting the modeled behavior. Young chimpanzees, for example, spend up to 5 years observing others and making unsuccessful attempts at cracking nuts without ever obtaining a reward (Inoue-Nakamura and Matsuzawa 1997; Matsuzawa et al. 2001), and a recent experiment suggests that chimpanzees "conform" to a tool-technique established in their group despite knowing an alternative technique capable of yielding equal rewards (Whiten et al. 2005). If social relations are important to social learning, this calls for experimental designs involving conspecific models rather than human models. Experiments using the latter cross-species arrangement have had mixed success (e.g., Bjorklund and Bering 2003; Nagell et al. 1993), and suffer from an obvious lack of ecological validity (de Waal 2001).

Social affiliations between model and observer are particularly important, since the opportunity to be near and observe others increases social learning opportunities (van Schaik 2003; van Schaik et al. 2003; Coussi-Korbel and Fragaszy 1995). Capuchin monkeys (*Cebus spp.*) are large-brained New World primates the groups of which are characterized by complex social relationships involving a remarkable degree of tolerance among unrelated individuals (de Waal 1997; de Waal and Berger 2000) within a loose dominance hierarchy, and provide a good model to address questions relating to social influences on behavior. Yet across a variety of contexts, the evidence for any social learning among brown capuchins has been mixed (Adams-Curtis and Fragaszy 1995; Custance et al. 1999; Ottoni and Mannu 2001; Visalberghi and Addessi 2001, 2003; Brosnan and de Waal 2004; Ottoni et al. 2005), which support the argument that perhaps capuchins are mainly being biased by the behavior of conspecifics, rather than specifically learning from them (Fragaszy and Visalberghi 2004).

The theoretical considerations and experimental evidence provided above lead to distinct predictions about the role that reinforcement plays on the choices made by captive capuchin monkeys in a foraging context. This experiment is designed as an exploratory study towards distinguishing between the different models. To do so we designed a simple task in which the rewards available to both models and observers varied systematically across conditions, such that rewards were available to neither, one, or both monkeys at different times during the study.

Methods

Subjects

Subjects included 18 (6 male and 12 female) adult brown capuchin monkeys (*Cebus apella*). Five females were pregnant and/or carrying a dependent offspring at some point during testing. The monkeys have lived in two social groups of 15 individuals each at the Yerkes National Primate Research Center, Atlanta, GA since 1991. The groups are housed separately in indoor/outdoor compounds measuring a total of 25 m^2 and 31 m^2 respectively. Purina High Protein Monkey Chow and water were available *ad libitum*, with fresh food trays containing fruit, vegetables, bread and protein solution provided each afternoon. Subjects were never food or water deprived.

Prior to testing, subjects and their dependent offspring were removed from the social group and transferred to a mobile test chamber (144 cm × 60 cm × 60 cm) with which the monkeys were familiar from previous experimental work (Brosnan and de Waal 2004; de Waal 2000). While in the test chamber, subjects had limited vocal, but no visual or tactile contact with the remaining members of their group. The test chamber was divided into two 72 cm × 60 cm × 60 cm sections, each occupied by only one monkey, and separated by a mesh partition which allowed visual contact, but prevented subjects from gaining access to the other's space. Monkeys could reach through the mesh front of the test chamber to access any materials placed in front of them. Following testing, subjects were returned to the social group.

Materials

The apparatus included a set of small wooden boxes (10 cm wide × 5.5 cm high × 6 cm deep), with hinged lids that could be easily opened by the monkeys. The boxes were painted using non-toxic spray paint such that each was distinctive in coloration and pattern (e.g., blue with white vertical stripes, black with yellow dots). For each condition, a unique set of seven boxes was created. Of these, three were designated as ‘‘target’’ boxes, in which a reward may be placed, and four were designated as ‘‘foils’’, and were always empty. Subjects were always presented with three boxes (1 target and 2 foils), spaced 6 cm apart and secured with a bolt and pin to a metal tray (51.5 cm wide × 6.4 cm high × 36 cm deep). The boxes could be opened, but not moved or removed by the monkeys. Between trials, however, the boxes could be quickly repositioned and interchanged by the experimenter.

Fruit Loops, a sugary cereal and highly preferred food (Brosnan and de Waal 2003), was the reward for respective trials. Because the odor of the cereal may have served as a cue as to which box contained a reward, a negligible amount (i.e., not enough for subjects to eat) of cereal dust was sprinkled into each box prior to each testing session.

All sessions were recorded by a Cannon GL1 digital video camera. Data were collected off videotapes by the experimenter and an independent coder.

Procedure

Model training

Six female monkeys (three from each social group) were designated as models at the start of the study. Models were never used as subjects, and vice versa. For each condition, each model was randomly assigned a different ‘‘target’’ box such that no two models from the same social group were trained to open the same box. Models were trained individually to search for and retrieve a food reward from only the target box to which she had been assigned. Training involved repeated presentations of the target box containing a reward in combination with two additional ‘‘foils’’ of varying patterns. The position of the target box was counterbalanced across trials, such that it was presented in each of the three positions with equal frequency. Training sessions continued until the model chose only the target box on 15 consecutive trials within a single session. To ensure that the models would continue to search the target box in the absence of reward (as required by the neither rewarded condition described below), a series of variable reward sessions, in which rewarded trials were randomly interspersed with between one and ten unrewarded trials, were conducted. This variable reward procedure is know to produce the highest rate of responding in traditional operant conditioning tasks (Skinner 1950). Training continued until each model chose only the target box on ten consecutive trials in two consecutive training sessions.

Despite extensive training one model failed to learn the task, and was therefore dropped from the study. In order to maintain a reasonable subject sample size, an additional monkey was not trained as a model. As a result, five subjects observed two models, and eight subjects observed three models.

Experimental tests

There were three experimental conditions, across which the rewards available to the model and subject varied: (1) neither the model nor the subject were rewarded at any time during testing (neither rewarded – *NR*), (2) only the model could be rewarded for correctly opening the box she was trained to explore, while the subject could not obtain a reward on any trial (model rewarded – *MR*), and (3) both model and subject were rewarded for exploring the target box (both rewarded – *BR*).

All subjects proceeded through each of the experimental conditions in order (NR, then MR, and finally BR), and completed each condition before moving on to the next. This within-subjects design was implemented to ensure that no rewards were associated with the apparatus in anyway prior to the NR condition. Within a condition, each subject observed separately two or three models from the subject's own social group for three consecutive sessions and then paired with the next model and so on. To account for effects of this repeated measures design, the order in which subjects were paired with models was randomized across subjects, and the model sequence for each subject was counterbalanced between conditions. Potential carryover effects among sessions or models observed are addressed statistically in the results.

Subjects completed only one session per day. Each session consisted of 12 alternating trials during which the subject first observed a model explore one of the three boxes (average latency to open <2 s). Next, the subject was presented with the same boxes, but randomly rearranged. In each trial, the apparatus was presented to the model, and then, following a 15 s inter-trial interval during which the boxes were repositioned by the experimenter, the apparatus was presented to the subject. Subjects could manipulate only one box per trial. If no choice was made within 15 s, or after a single box was manipulated, the apparatus was withdrawn. Under all experimental conditions, boxes were baited and repositioned out of view of both monkeys, and box positions were counterbalanced across each session such that within a session the target box was located in each of the three possible positions (left, center and right) with equal frequency.

For consistency, we analyzed data from only the first two models observed by all subjects. It should be noted that this did not alter the outcome of the study: whether conditions were compared using the two-model data (as done here) or including all three models for subjects exposed to these, did not alter any of the conclusions reported below. As a result, in each of the three reward conditions, the data presented and analyzed represent 6 total sessions- 3 sessions with each of two different models. In total per subject, the data include 36 trials with each model, for a total of 72 trials per condition.

Second model rewarded condition

To test specific predictions about long-term effects of rewards on subjects' behaviors, the model rewarded (MR) condition was repeated after the third individual learning session. That is, we were interested in whether or not subjects' performance would decrease when rewards were no longer available to themselves. If the success of subjects resulted only from experience with the testing paradigm, absence of reward should have no effect on subjects' performance. Accordingly, a new set of boxes was created, models retrained, and subjects were paired with models in an order identical to the original MR condition.

Rewarded controls

We also investigated how efficiently subjects would learn to associate a specific box with a reward without the benefit of a model. Subjects were first tested in the 'individual control' (with no other monkey present), and later in the presence of the same partner normally serving as model (but this time without an opportunity to actually model behavior; 'partner control'), a situation more comparable to the experimental conditions. Each session consisted of 12 trials in which a target box was baited with a reward and presented to the subject in combination with 2 (of 4 available) foil boxes, which did not contain a reward. As with experimental tests, the subject had a maximum of 15 s to explore and obtain a reward from only one of the three boxes.

A total of six control sessions were conducted. In the individual control (sessions 1–3), all 13 subjects were tested without a partner at the conclusion of each experimental condition (the first after the neither rewarded (NR) condition, the second after the model rewarded (MR) condition, and the third after the both rewarded (BR) condition). The same boxes were used in all three sessions. In order to address the confound that in the above controls no partner was present, we conducted three partner control sessions 24 months after the experimental series, using all subjects ($n = 6$) still available at that time. Subjects (three male and three female) were tested with a partner in the adjacent section of the test chamber. A novel set of boxes were used in each session.

These two sets of controls differ in two ways. The individual control was conducted without a partner and reused the same boxes across three sessions, which means that learning is expected across the series in the same way as across the BR series of experiments (the only condition in which subjects received rewards). The partner control was conducted in the presence of a partner, but now with new boxes in each session, so that no learning across the three sessions is expected. As a result, we pooled the data for all three sessions, and compared this to the pooled data from the first exposure of boxes in the experimental series in which subjects were rewarded, i.e., the first BR session.

Unrewarded control

It is possible that subjects were using an alternative strategy, one that has nothing to do with social influences, to direct their choice. In each of the previously described conditions, the target box (i.e., the box that models had learned to open or, in individual learning sessions, the box that contained a reward) was presented to subjects on every trial, whereas the four foil boxes alternated across trials, hence were presented less frequently than the target box. As a result, subjects may have not have attended to the behavior of the model, but instead may have directed their choice towards the box that appeared most often.

To test this alternative explanation, an unrewarded control session (of 36 trials) was run approximately 18 months after the experimental tests with the six subjects still available at the time of testing. A new set of boxes was created, and included one target and four foils, of which none could contain a reward. Although no model was present, control trials were otherwise identical to experimental trials, such that the apparatus was first positioned for 15 s in front of the area in which otherwise a model would be. The boxes were then rearranged, and presented to the subjects. Subjects had up to 15 s to make a choice, after which the boxes were withdrawn and arranged for the next trial. In this way, subjects were exposed to the boxes for an equivalent amount of time as in experimental conditions, with the only difference being that no model was present to make a choice among them.

Measures

The primary dependent variable was the number of trials in which the subject matched the choice of the model, and in individual learning sessions the number of trials in which a reward was retrieved or target box chosen, expressed as a percentage of total responses made by the subject in each session. Trials in which a subject did not make a choice were not counted, and as a result, the number of responses made in a session could range from 0 to 12. In addition, for each trial, the positions of the boxes and the location (left, center or right) of the box chosen by the models and subjects were also recorded.

Results

The data for each social group were initially analyzed with an analysis of variance (ANOVA), with a crossover design. This crossover analysis allowed us to rule out effects due to the identity of a model (i.e., ‘A’ and ‘B’) or the order in which each model was observed (e.g., ‘A’ then ‘B’ versus ‘B’ then ‘A’). Although some subjects copied the choice made by the model more in the third session with each model, we found no evidence to support the hypothesis that repeated testing within a condition was a significant factor in our results. With respect to model order or identity, no significant findings were obtained.

Since we observed no systematic differences between the two social groups, and no differences when the data for the third model was excluded, data for all 13 subjects were combined into a repeated-measures ANOVA that included two within-subjects variables (the three reward conditions and three test sessions per condition) and two between-subjects variables (the two social groups and two sexes). The results confirmed that the groups did not differ statistically from one another ($F_{1,9} = 2.09$, $P = 0.183$).

There was a significant main effect of reward condition ($F_{2,36} = 28.14$, $P < 0.001$), and within-subjects contrasts revealed that subjects matched the model’s choice more often when both individuals were rewarded, the both rewarded (*BR*) condition ($M = 70.8\%$, SD = 14.6%) than in the neither reward (*NR*) condition ($M = 44.6\%$, SD = 12.5%) or model rewarded condition ($M = 46.1\%$, SD = 13.7%), whereas the latter two conditions did not differ significantly from one another. An interaction between reward and session was also found ($F_{4,36} = 12.66$, $P < 0.001$). As can be seen in Fig. 1, this interaction reflects the BR condition, in which subjects showed a significant increase in matching from session 1 to 3 ($F_{2,36} = 18.59$, $P < 0.001$).

We found a significant sex by reward interaction ($F_{2,36} = 5.59$, $P = 0.01$). In the BR condition, females ($M = 78.5\%$, SD = 7.5%) matched the choice made by the model on significantly more trials than males ($M = 61.8\%$, SD = 1.6%). There were no differences between males and females in any other conditions.

Comparison to chance performance

We tested if subjects chose the same box as the model more often than expected by chance. For each session of each reward condition, the mean proportion of trials in which subjects copied the choice made by a model was compared to a test statistic of 33.3% using a two-tailed one-sample *t* test. The results are presented in Table 1 and show that in all but one session (NR2), subjects copied the choice of the model at a level above chance.

Location

Our study was designed with stimulus enhancement in mind, but it was possible that capuchins chose the box presented in the same location, as opposed to the same color, as the model. To test this hypothesis, the number of trials in which subjects chose a box in the same location as the model were tallied, and compared to a test statistic of 33.3% in a one-sample *t* test (two-tailed). There were no significant effects in any of the NR or MR sessions (NR1: $t_{12} = -0.32$, $P = 0.76$; NR2: $t_{12} = 0.47$, $P = 0.65$; NR3: $t_{12} = -0.21$, $P = 0.84$; MR1: $t_{12} = -1.71$, $P = 0.11$; MR2: $t_{12} = -1.11$, $P = 0.30$; MR3: $t_{12} = -1.08$, $P = 0.30$). But, in all three BR sessions (Mean matching rate = 25.2, 27.2, 26.7% respectively) subjects significantly less often chose the box in the same location as the model's choice (BR1: $t_{12} = -3.08$, $P = 0.01$; BR2: $t_{12} = -3.94$, $P = 0.002$; BR3: $t_{12} = -4.19$, $P = 0.001$). These findings are likely due to the fact that subjects found the reward in a high proportion of trials, and that the target box was rarely located in the same position for the subject as it was for the model.

Table 1 Average (+SD) proportion (expressed as a percent) of trials in which subjects copied the choice made by a model for three sessions of each reward condition

Condition	Session	*M*	SD	*t*	*P*
NR	1	42.0	13.4	2.423	0.032
	2	44.4	21.5	1.917	0.079
	3	47.3	18.3	2.811	0.016
MR	1	46.6	15.3	3.208	0.008
	2	43.9	16.3	2.421	0.032
	3	47.9	19.9	2.685	0.020
BR	1	48.7	14.6	3.874	0.002
	2	73.7	24.1	6.097	<0.001
	3	90.0	10.9	18.768	<0.001
2nd MR	1	52.5	26.4	2.517	0.029
	2	62.6	20.1	5.044	<0.001
	3	54.7	20.6	3.584	0.004

Data on all subjects were compared to chance (33.3%) using one-sample *t* tests (two-tailed), $df = 12$, $\alpha = 0.05$

NR Neither rewarded, *MR* Model rewarded, *BR* Both rewarded

Second model rewarded condition

In the second round of testing the model rewarded (MR) condition (Fig. 1), subjects copied the model's choice in fewer trials than in the both rewarded (BR) condition. These findings were analyzed with a repeated-measures ANOVA in which reward (MR, BR,

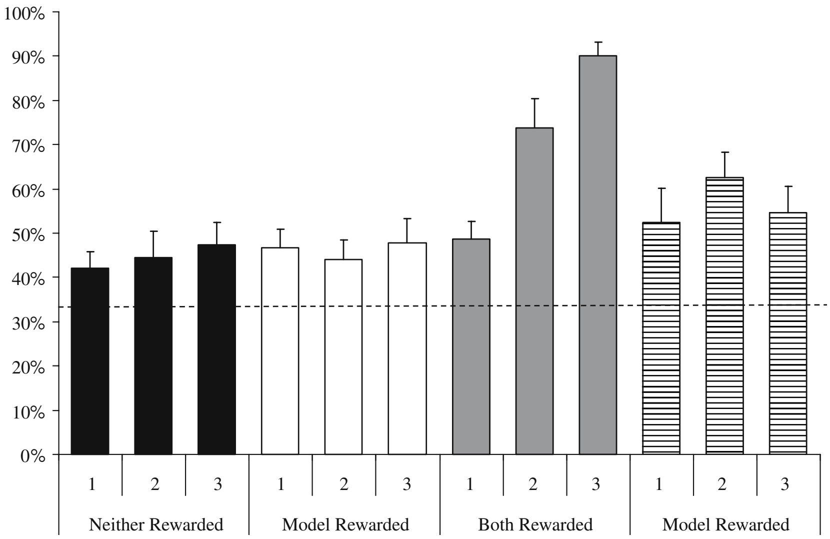

Fig. 1 Average (+SEM) proportion of trials in which subjects ($n = 13$) chose the same box as demonstrated by a conspecific model in three conditions: neither monkey was rewarded, only the model was rewarded, and both monkeys were rewarded. *Bars* represent each of three sessions per condition

and the second MR) and session were within-subjects factors. There were significant effects of reward condition ($F_{2,22} = 11.62$, $P < 0.001$) and session ($F_{2,22} = 12.10$, $P < 0.001$), and a significant reward condition by session interaction ($F_{4,44} = 11.07$, $P < 0.001$). With respect to reward, within-subjects contrasts revealed that mean matching was significantly higher in BR than second MR ($F_{1,11} = 8.80$, $P = 0.01$). No significant differences were found between first and second round of MR testing.

Rewarded controls

In the individual control sessions, in which the location of a reward could be discovered without the benefit of a model, subjects showed variable success in locating a reward (Fig. 2). As expected, we found evidence of learning across the three sessions, in that subjects performed significantly above chance (33.3%) in the two later sessions, but not in session 1 (two-tailed, one-sample *t* test; Session 1: $t_{12} = 0.385$, $P = 0.71$; Session 2: $t_{12} = 3.11$, $P = 0.01$; Session 3: $t_{12} = 6.24$, $P < 0.001$). The data were also compared to the data of the both rewarded condition with a repeated measures ANOVA. Condition had no significant effect ($F_{1,24} = 4.49$, $P = 0.056$). Yet, as can be seen in Fig. 2, in all three sessions subjects located the reward more often after observing a partner find the reward (both rewarded), than when no partner was present (individual control).

For the partner control tests, new boxes were presented in each session. Therefore, the data for the three partner control sessions were pooled for all subjects, and compared to the findings in the first session of the both rewarded condition for the same individuals (6 of the original 13 subjects). Subjects located the reward significantly more after observing a partner than when the partner was present, but not active (Paired-sample *t* test: $t_5 = 3.54$, $P = 0.02$).

Unrewarded control

For each subject, the number of trials in which the target box (which appeared on all trials) was chosen was recorded. In these tests, no partners were present, but target boxes and foils were alternated in the same way as in social learning trials. Subjects chose the target box on an average of 33.1% (SD = 8.6%) of trials on which a choice was made, which did not differ significantly from chance (two-tailed one-sample *t* test: $t_5 = –0.062$, $P = 0.47$).

Discussion

When Galef (1992, p. 171) claimed that “although imitation might introduce some novel behavior into the repertoire of members of a population, through time this behavioral novelty would be maintained, modified, or extinguished depending on its effectiveness (relative to available variants) in acquiring rewards,” he expressed the prevailing opinion that while social partners can influence the behavior of an individual,

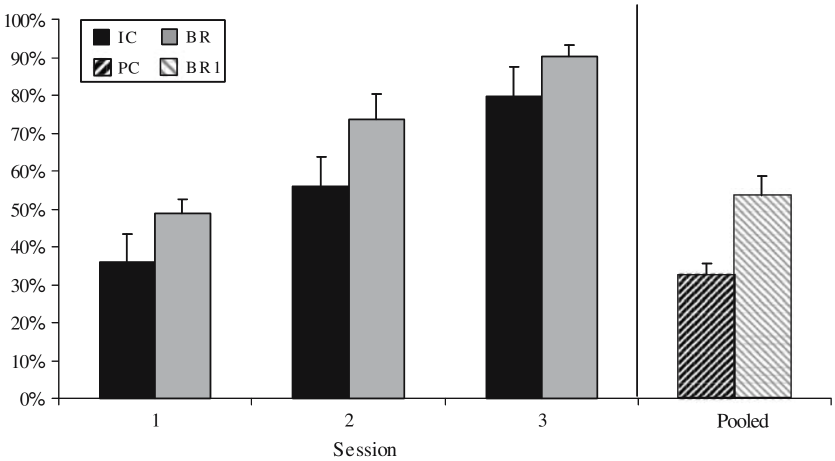

Fig. 2 Average (+SEM) proportion of trials in which subjects located a food reward in conditions in which subjects were rewarded. Individual control sessions (IC *black bars*), were compared to the three sessions of the both rewarded condition (BR *gray bars*), and include data for 13 subjects. In IC sessions, subjects were tested in the absence of a social partner, and sessions were interspersed among social learning conditions. In the partner control (*black hatched bars*), conducted 24 months after the study had been completed, subjects ($n = 6$) were tested in the presence of a social partner and new boxes were presented in each session. The data for three partner control sessions were pooled and compared to the performance of the same subjects in the first session of the both rewarded condition (*gray hatched bars*)

learning is ultimately guided by the tangible rewards it produces. If self-reward was the only factor affecting the behavior of capuchin monkeys in this context, then subjects would show a significant preference for the target box only on trials in which a reward could be obtained (i.e., in the both rewarded condition and rewarded controls), but not in unrewarded conditions. Our data show that while self reward enhanced the bias towards a specific box, rewards alone do not offer a complete explanation for our findings. Subjects were also choosing the same box as a model on more trials than was expected by chance in the neither rewarded (NR) and model rewarded (MR) conditions, when rewards could not be obtained. In addition, we found no evidence of extinction of this bias, in that the preference shown by subjects for the modeled box persisted across the first two conditions. Overall, the predictions generated by the Reinforced Observational Learning Model (ROLM) were not entirely supported by our findings.

With respect to the predictions of Vicarious Reinforcement Model (VRM), we found that compared to the neither rewarded condition, observing a conspecific retrieve a reward in the model rewarded condition did not enhance the subjects' performance. Although rewards for the model may have enhanced the attention paid by subjects to a particular box, the addition of a reward for the model did not result in a greater bias by the subject towards the box explored by the model. Even when capuchins were rewarded for their choice, as in the BR condition and both rewarded controls, subjects located the reward more often in the presence of an active partner than when tested alone or with a passive partner. Together our findings suggest that one or more alternative factors, which have little or nothing to do with extrinsic reward, are at work.

Perhaps capuchins were copying the choice made by a familiar conspecific in a manner similar to the imitative attempts to crack nuts by young chimpanzees (Matsuzawa et al. 2001), which they do without any success in the first couple of years, hence without ever procuring a reward. These and other similar examples led to de Waal's (2001) Bonding-and Identification-based Observational Learning model (BIOL) in which social relations, rather than rewards, are stressed. For example, the transmission of a grooming culture among captive chimpanzees was correlated with measures of proximity and affiliation (Bonnie and de Waal 2006), and among wild chimpanzees daughters more reliably copy the ant-fishing technique of their mothers than do sons, perhaps reflecting the daughters' identification with their mothers (Lonsdorf et al. 2004). In the both rewarded (BR) condition of the present study, female subjects copied the choice of another female on more trials than did males, suggesting that sex identification may have played a role here as well. However, additional analyses of the data are needed to fully address whether copying by capuchins was affected by the social relationship (e.g., kinship, age, dominance) between model and observer.

The design of this repeated measures study is not without limitations. Because all subjects went through experimental conditions in order, the results obtained from later conditions may have been confounded by subjects' experiences in prior conditions. However, for the following reasons we believe this is not the case. First, for each condition a new set of boxes was created, so that subjects needed to attend to and react to novel stimuli across conditions. If performance in one condition carried over to next, we expect linear increase across experimental conditions. However, we found no statistical difference between the neither rewarded (NR) and model rewarded (MR) conditions. Moreover, bias resulting from model's choice was apparent from the beginning - subjects chose the same box as the model at a level greater than chance in the first (NR) condition. Finally, subjects copied the choice of a model less in the second MR condition, which followed the both rewarded (BR) condition. If the rewards of the BR condition had significant long-term or carry-over effects, we would have expected to see no decrease in the second MR condition. Instead, the proportion of trials in which subjects chose the modeled box returned immediately (in the first session) to the level observed in the original MR condition.

Irrespective of reward, the actions of a conspecific likely served to draw the attention of subjects to certain stimuli, a phenomenon known as stimulus enhancement (Spence 1937), and included in socially-biased learning (Fragaszy and Visalberghi 2001, 2004). Moreover, capuchins appeared to be attending to the more salient cue, the color as opposed to location, of the box chosen by the model to guide their search strategy. The enhanced attention paid to those objects by others may provide a critical precondition for more complex social learning. However, our experimental set-up was not designed to address more than stimulus enhancement, hence we do not have the evidence for nor make a claim that other learning mechanisms were at work. Yet there remains a possibility that the affects we have attributed to social influence could have been produced in other ways. For instance, if the same effects are found when capuchins observe boxes opening in the absence of a social agent, or 'ghost control' (Fawcett et al. 2002), or if a human model was equally influential, then the affects conspecifics have on another capuchin's behavior would be questioned. Although the present study did not test either of these possibilities, future work could be directed towards these alternative explanations.

In conclusion, capuchin monkeys do not need to be rewarded—and in fact do not even need to see any rewards—in order to be influenced by the foraging behavior of others. Their tendency to copy others thus seems independent of reward, even though our study also shows that when self-reward is added the bias to search where a model had searched turns into a robust effect well beyond that shown without self-reward.

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