Socially Learned Preferences for Differentially Rewarded Tokens in the Brown Capuchin Monkey (*Cebus apella*)

Sarah F. Brosnan and Frans B. M. de Waal
Yerkes National Primate Research Center and Emory University

Social learning is assumed to underlie traditions, yet evidence indicating social learning in capuchin monkeys (*Cebus apella*), which exhibit traditions, is sparse. The authors tested capuchins for their ability to learn the value of novel tokens using a previously familiar token-exchange economy. Capuchins change their preferences in favor of a token worth a high-value food reward after watching a conspecific model exchange 2 differentially rewarded tokens, yet they fail to develop a similar preference after watching tokens paired with foods in the absence of a conspecific model. They also fail to learn that the value of familiar tokens has changed. Information about token value is available in all situations, but capuchins seem to pay more attention in a social situation involving novel tokens.

Social learning, or the ability to learn from others (Whiten, 2000), is in evidence in many animal species. Such diverse taxa as birds (Campbell, Heyes, & Goldsmith, 1999; Midford, Hailman, & Woolfenden, 2000; Templeton, Kamil, & Balda, 1999; Zeltner, Klein, & Huber-Eicher, 2000), fish (Laland & Williams, 1997; Reader & Laland, 2000), and mammals (Pongracz et al., 2001; Previde & Poli, 1996; Zentall, 1996) have displayed social learning. Recently, there has been a surge of interest in how socially learned behaviors may lead to the development of "traditions" or "culture" (Panger et al., 2002; Perry et al., 2003; Perry & Manson, 2003; van Schaik et al., 2003; Whiten et al., 1999). Traditions are typically defined as socially transmitted long-term behaviors exhibited by some social groups of a species, but not others, and in which the presence or absence of the behavior is not due to ecological conditions (Perry & Manson, 2003; van Schaik et al., 2003; Whiten et al., 1999). The existence of different tradition-based cultures within the same species has been explicitly examined in several long-term field studies of primates. Among the great apes, both chimpanzees (Whiten et al., 1999) and orangutans (van Schaik et al., 2003) exhibit cultural behavior. However, the concept seems applicable to a wide range of other animals, including the New World primate genus that is the subject of the present study, the capuchin monkey (Ottoni & Mannu, 2001; Panger et al., 2002; Perry et al., 2003; Perry & Manson, 2003).

The capuchin monkey is a particularly intriguing addition to the list, as references to culture and social transmission of knowledge are more prevalent with regard to great apes and Old World monkeys (Huffman, 1996; Itani, 1958; Kawai, 1965). However, a recent cross-site comparison of white-faced capuchin (*Cebus capucinus*) groups living at different locations within close proximity of each other in a similar habitat (tropical dry forest) in northwestern Costa Rica has proposed more than 25 different traditions. These include differences in foraging behavior (Panger et al., 2002), interspecific interactions, and social conventions (Perry et al., 2003; Perry & Manson, 2003). Furthermore, nut cracking, a behavior documented as cultural in chimpanzees (Whiten et al., 1999), has also been found in one population of brown capuchins (*Cebus apella*) living in semiwild conditions in Brazil. These capuchins apparently spontaneously developed the behavior of using stones to crack wild Syagrus nuts, and the transmission of nut-cracking ability appears to have a social component (Ottoni & Mannu, 2001).

One difficulty in documenting traditions is that the underlying mechanism of social transmission (i.e., social learning) is difficult to verify in the field or replicate in captivity. This is due at least in part to inherent difficulties with both laboratory work and documenting social transmission in the field, and it weakens the case for socially transmitted traditions. Looking exclusively at capuchin monkeys, there are indications for social transmission of nut-cracking behavior in semiwild capuchins (Ottoni & Mannu, 2001), yet no evidence indicating social transmission of the same kind of behavior has been found in the laboratory (Visalberghi, 1987). Furthermore, even individuals who exhibit social learning in some situations may not do so in other, seemingly related, instances. For instance, capuchins imitate some components of food handling in the laboratory (Custance, Whiten, & Freedman, 1999) and vary on the processing of approximately 20 known foods in the field (Panger et al., 2002); however, another aspect of food acquisition, food palatability information, appears to be the result of general-

ized reduction of neophobia in the presence of conspecifics rather than more specific social transmission (Addessi & Visalberghi, 2001), and capuchins apparently do not socially learn that familiar foods have been adulterated (Visalberghi & Addessi, 2000).

It is difficult to interpret such contradictory research outcomes, yet it would be surprising if social learning was absent in captive capuchin monkeys given that their wild counterparts demonstrate such an abundance of traditional behavior. Furthermore, capuchin monkeys exhibit characteristics that would seem to favor social learning. They spend a relatively long time dependent on their mother (Freese & Oppenheimer, 1981), they are tolerant enough to allow food sharing and cooperation (de Waal, 1997; de Waal & Berger, 2000), and they exhibit a varied, omnivorous diet in the wild (Freese & Oppenheimer, 1981), which provides ample opportunity and functionality for social transmission of food knowledge. Failure to find social learning in captivity may relate to the difficulty of the tasks used, lack of appropriate long-term exposure (at least compared with the level at which wild capuchins are exposed to each other's behavior), the experimental task's lack of saliency for the individuals performing it, or the availability of nonsocial cues in some situations. Thus, we decided to test captive brown capuchins for social learning in preference formation, using a simple task with which they were extensively familiar.

Previously, the capuchins in this study had participated in a simple barter economy using an exchange task (Brosnan & de Waal, in press). For this task, capuchins were initially conditioned that different tokens were worth different foods, some highly desirable and some less so. The capuchins quickly learned to prefer the token associated with the higher value food over that associated with the lower value food. Furthermore, although preferences were weaker for tokens than for the foods themselves, the monkeys chose the high-value token over the low-value token in 78% of choices (Brosnan & de Waal, in press).

Knowing that monkeys form preferences for tokens after individual interaction with the experimenter, we examined whether they would develop a preference for the token worth a higher value food after watching a conspecific partner exchange with two novel tokens. Furthermore, to distinguish between information transmitted via a conspecific versus information transmitted via the association of the tokens, we also ran a nonsocial control test in which no partner was present but in which rewards and tokens were viewed in association. Thus, we could determine the importance of a conspecific model in social learning. Finally, on the basis of earlier findings that capuchins do not change behavior toward familiar food that has been negatively altered after watching a conspecific interact with it (Visalberghi & Addessi, 2000), we examined whether watching a conspecific partner exchange using familiar tokens with reversed values would induce individuals to modify preexisting preferences.

This study was somewhat different from previous laboratory studies on capuchins. First, we did not attempt to teach the monkeys a new task or skill. The subjects were only required to gain information that was previously shown to be valuable (i.e., information that could help them garner more food rewards) and apply it in a familiar paradigm. Whereas some species appear to socially learn complex behavioral repertoires in the field, such as nut cracking (Boesch & Boesch, 1983), these behaviors are unlikely to emerge after the relatively brief exposures to novel behavior typical of social learning experiments in the laboratory (de Waal,

2001). By using a thoroughly familiar exchange task, which these monkeys had worked on continuously for 12 months previous to the present variations of the task, we were hoping to overcome the handicap of arbitrarily short exposure times common in laboratory experiments. Furthermore, the study differed from many social learning experiments (Tomasello, Savage-Rumbaugh, & Kruger, 1993; Custance et al., 1999; Whiten, Custance, Gomes, Teixidor, & Bard, 1996) in that subjects were presented with a conspecific rather than a human model.

The nature of the task also made our experiment salient to the experiences of capuchins in the wild. Many of the foodstuffs these monkeys consume are difficult to extract from their packaging (Freese & Oppenheimer, 1981; Janson, 1998; Ottoni & Mannu, 2001); hence, wild capuchins may learn which unlikely places to search for food by watching the choices of conspecifics. Likewise, in our situation the high-value food reward was somewhat difficult to procure (the right token had to be returned) and the subject could most easily learn the "correct" choice (e.g., the higher value token) by observing a conspecific's interaction with the tokens. In fact, subjects in our study did not receive rewards and thus had to gain any information from observation alone.

We hypothesized that capuchins could learn the value of tokens through some form of social transmission. Specifically, we predicted that capuchins would learn to prefer the higher value of a pair of novel tokens after watching a conspecific partner exchange. Furthermore, if the above learning is purely a matter of association between token and food reward, the learning of a preference through the pairing of a token with its reward should be just as efficient in the presence of a social partner as without one. On the other hand, if such learning requires a conspecific to be present for whatever reason, learning of the preference should occur in the social context only. The latter is predicted by the bonding- and identification-based observational learning model (BIOL), which emphasizes the socioemotional component of cultural learning (de Waal, 2001). Finally, we predicted that in accordance with previous findings by Visalberghi and Addessi (2000), capuchins would not switch preferences for tokens for which they had previously formed preferences.

Method

Subjects

The subjects included 8 brown capuchin monkeys from two social groups at the Yerkes National Primate Research Center, in Atlanta, Georgia. These included 1 adult male, 2 subadult males, and 5 adult females. All but one of the adult females were pregnant and/or carrying a dependent offspring at some point during testing. All subjects had previously been used in the exchange study on which the current study is based (see Brosnan & de Waal, in press).

The subjects lived in groups housed in two large, indoor–outdoor enclosures. Each enclosure contained ample three-dimensional climbing space as well as trapezes, perches, and enrichment items. Purina Small Primate Chow was provided twice a day, at approximately 0930 and 1730. A tray consisting of fruits, vegetables, and bread with a protein solution was provided to each group every day at approximately 1730. Running water was available ad libitum. This feeding schedule was followed regardless of the day's testing, and subjects were never food or water deprived. For more details about the testing facility, see de Waal (1997).

The subjects had previously been trained to enter transport cages, which allowed us to place them into a test chamber. Individuals were comfortable

with this procedure and were well habituated to the test chamber. The test chamber was divided by a mesh partition into two equal sized (36 × 60 × 60 cm) compartments, such that subjects had visual, vocal, and limited tactile access to a conspecific in the other compartment but could not physically interfere with the other's interactions with the experimenter. For testing, subjects were enclosed in one compartment while the other compartment either contained the model monkey or was empty. The test chamber was backed by an opaque panel so that subjects had vocal contact but no visual or tactile contact with their group while in the test chamber. This allowed experimenters to interact with subjects in a controlled manner with minimal distractions. Dependent offspring were always allowed into the test chamber with their mothers. No subject was ever involved in more than one test on any given day.

Models

One familiar individual was the model for all subjects from the same social group. Because subjects came from two groups, we used two models, each acting as the model for all subjects from their own social group. In both cases, these models were high-ranking adult males. We chose to use the same individuals as models for all subjects, both for consistency and to ensure that no models were ever used as subjects. Dominant males were chosen so that the dominance direction (although not necessarily the rank difference) was consistent across all model–subject pairs. No other subjects were tested as models. Likewise, models were never used as subjects in the present experiments, but they had fully participated in the previous exchange study and thus were as familiar with the test paradigm as were the subjects. The models were exposed to each pair of novel tokens prior to demonstrating exchange to the subjects, so the tokens were never novel to the models during any test session.

Exchange Paradigm

For this study, exchange was operationally defined as the subject returning an inedible token to the experimenter, for which the subject received a food reward. Subjects had been taught this behavior in earlier studies (see Brosnan & de Waal, in press). To begin an exchange, the experimenter would stand in front of the monkey, with the left hand outstretched in a begging gesture. The palm of the hand was approximately 5 cm above the floor of the test chamber and the tips of the fingers were approximately 2 cm from the mesh. The right hand was placed in the pocket of the experimenter's lab coat. The monkey had to place the token being exchanged into the palm of the experimenter's outstretched left hand. Throwing the token at the experimenter, into the experimenter's hand, or out of the test chamber did not count as exchanges.

When the token had been returned, the experimenter held it up in front of the exchanger but out of reach of the monkey, then lifted the correct reward from a bowl visible to both monkeys and gave it to the exchanger. During trials, rewards were kept in separate containers at the same height as the floor of the testing chamber, approximately 10 cm away (i.e., out of the monkeys' reach), between the capuchins. For consistency, the reward containers were always in the same position relative to the subject, with the higher value reward closer to the subject. Exchange interactions were typically completed in approximately 10 seconds.

Most of the data were collected live during testing by a second experimenter and verified afterwards. All sessions were videotaped and timed to a hundredth of a second on a digital video recorder.

Token Preference Tests

We determined token preferences by giving the subjects 10 successive trials in which they could choose to take one of two tokens. The chosen token was considered to be the preferred one. For each trial, the experimenter held one token in each hand at eye level for the capuchin subject, approximately 10 cm apart, in front of the same two square openings in the mesh in the front of the test chamber and outside of the enclosure, approximately 5 cm away from the mesh. To choose a token, the subject had to reach out and actively take a token from the experimenter. Token placement was counterbalanced between trials, such that each token alternated between presentation on the left and right. This was done to control for any side biases in subject choice. During token preference tests, the experimenter wore a surgical mask covering the nose and mouth and a clear but reflective face shield covering the entire face (standard garb at Yerkes), thus it is unlikely that subjects were responding to unintentional facial cues by the experimenter. Furthermore, rewards were held in front of the same two square openings to minimize unintentional biasing by presenting either token in a place more convenient to the subject.

This paradigm has previously been used to assess both food and token preferences (Brosnan & de Waal, in press; de Waal, 1997). It appears to be consistent with the subject's preference for the token and produces stable preferences over extended time periods (Brosnan & de Waal, in press). For this study, we gave token-preference tests prior to and following observation of the model exchanging to determine both their pretrial and posttrial preferences for the different tokens. For any pair of tokens for which the mean initial preference across subjects deviated by more than 10% from chance (e.g., preference for one token was below 45% or above 55%), it was assumed that there was an intrinsic token preference. Such an intrinsic preference was found for only one token pair, and both tokens were abandoned for further testing. Hence, all tests were conducted with pairs of tokens with little difference in mean preference. An exception was the value reversal test (see below), in which we expected a preexisting bias for one token.

To the best of our knowledge, all tokens used were novel to the capuchins. They had never experienced them in previous studies of any kind in our lab and never saw any token in more than one session during the course of testing. Tokens were as different as possible considering Institutional Animal Care and Use Committee guidelines (i.e., no sharp edges, nontoxic, too large to swallow, indestructible) and practical constraints (i.e., small enough to fit through the mesh). A variety of metal, hard nylon, and polyvinyl chloride (PVC) hardware items were used for the tests including nuts, bolts, washers, carriage bolts, screws, hooks, small pipes (bent and straight), and spacers. These tokens were put in pairs of approximately equal-size items but always differing in form and material. Although all subjects within a given session saw the same pair of tokens, no token was ever used in more than one session for any individual. Thus, subjects were choosing between two novel tokens for each test session (excepting the value reversal test).

Social Learning Test

We tested the ability of subjects to learn the value of a token by watching a conspecific partner exchange. All testing took place in the test chamber, with the subject and model separated from each other by the mesh partition. Prior to each test session, one token from the novel pair was randomly assigned as the high-value token. This pairing was used for all subjects within that test. High-value tokens were paired with Froot Loops (a sugary, fruit flavored, dry breakfast cereal approximately 1 cm in diameter), a highly preferred food item familiar to the monkeys, whereas the other token became a low-value token, paired with 1.5- × 1.5-cm squares of green bell pepper, a nonpreferred but accepted food item (Brosnan & de Waal, in press).

Each social learning session consisted of an initial token-preference test, following by the model exchanging, and ended with a second token-preference test. Subjects participated in four sessions, with each session utilizing a pair of novel tokens. Subjects were initially given a token-preference test for determination of their baseline preferences for each token. This test consisted of 10 choices between the two novel tokens. Subjects were not given any food rewards during this time, and the

experimenter collected all tokens from the test chamber prior to the model's exchange session.

Following this, the subject saw the model exchange 10 of each token (for a total of 20 exchanges). This was divided into two trials, each with only 10 tokens (5 of each) to guarantee that the subjects saw both tokens returned in both halves of the model's exchange. We did not otherwise attempt to control the order in which models returned the tokens but allowed them to exchange in whatever order they preferred, to assure that the models' behavior was as natural as possible. Subjects appeared to pay attention to all exchanges, orienting toward the model and the presented rewards. When a token was returned, the experimenter held it up, lifted the reward to join it, then gave the reward to the model. Thus, the subject was easily able to see which token had been returned, as well as the corresponding reward. Models typically did not return the tokens in any specific order. The subject was given no rewards during this session.

Immediately following the completion of all 20 exchanges by the model, a second token-preference test was given to the subject for determination of their preferences for each token after having seen the model exchange. This test also consisted of 10 choices between the two tokens. Once again, subjects received no rewards during this test. We measured the subjects' change in preference for the designated high-value token between the first token-preference test, when the tokens were novel, and the second token-preference test, when the subjects had seen the model exchange with the tokens and thus could have formed a preference based on their observation.

Seven subjects completed all four of the social learning sessions, and 1 subadult male completed only two sessions (for a total of 8 subjects tested). This male was included in the social learning analyses because he also completed all nonsocial transmission test sessions.

Nonsocial Transmission Test

We ran nonsocial transmission tests to determine whether capuchins could develop a preference for a token after seeing that token paired with a reward without a conspecific model being present. This test was identical to the test above, except that no model was present in the other side of the test chamber. Instead, each token was held up 10 times in a predetermined random order, and while the token was lifted, the reward was held up and moved as if to reward the nonexistent "model." Then both the token and the reward were returned to their respective containers. Thus, subjects saw the rewards for approximately the same length of time and in the same relationship to the token as they did in the social learning tests. The only difference was that no conspecific received or consumed the reward. Once again, we measured the subjects' change in preference for the designated high-value token between the first token-preference test, when the tokens were novel, and the second token-preference test, when the subjects had seen the tokens paired with their respective rewards and thus could have formed a preference based on their observation of this association. Nonsocial transmission tests were done following the completion of the social learning tests. All 8 subjects received two nonsocial transmission sessions, each with a pair of novel tokens.

Value Reversal Test

We ran value reversal tests to see whether capuchins could alter a preference previously established via individual learning for tokens after watching a partner exchange the familiar tokens for different rewards. Unfortunately, as this test relied on previous strong value associations, it could only be run once per animal, using the one pair of tokens for which they were known to show a long-term, strong preexisting preference. This was the only session in which subjects saw a token they had previously encountered. The token pair had been used continuously for approximately 6 months in a previous study (Brosnan & de Waal, in press). This preference was expected to be somewhat weaker than it had been previously, as several months had elapsed since initial testing during which the

subjects had been exposed to other token pairs in the social learning and nonsocial transmission tests. Thus, we performed the initial token-preference test to verify subjects' continued preference for the original high-value token (which would be evidenced as a lower than chance preference for the current high-value, but former low-value, token in the initial token-preference test).

For this test, we used the washer and pipe combination that had been used in the previous barter test (Brosnan & de Waal, in press). In the previous experiment, the washer was the preferred token, worth a Froot Loop, and the pipe was the less preferred token, worth a piece of bell pepper. We reversed the reward associations for this test, such that the pipe was worth a Froot Loop and the washer was worth a piece of a bell pepper. The procedure for this test was identical to that of the social learning test. Seven subjects participated in this experiment. We measured the subjects' change in preference for the designated high-value token between the first token-preference test and the second token-preference test, when the subjects had seen the model exchange with the tokens and thus could have changed their preference on the basis of their observation of the model's exchange. Value reversal tests were run after all other tests were completed.

Statistics

We analyzed the data using a heterogeneity G test (Sokal & Rohlf, 1995) to compare the capuchins' preference for the high-value token in the second Token Preference test to their original preference for that token in the initial token-preference test. This test allowed for comparison of individual preferences rather than a change in pooled preferences and allowed us to test whether subjects are significantly homogeneous in their behavior before analyzing their changing preferences. We used the pooled mean of the subjects' initial preference for the high-value token (e.g., the initial token-preference test) as the null hypothesis. For the social learning and nonsocial transmission tests, this was quite close to 50% (chance), but it differed from chance in the value reversal test, as subjects had previous experience with the tokens.

Following our determination of the null hypothesis, we compared the subjects' preferences for the designated high-value token in the second token preference test to the initial preferences. Each subjects' choices were pooled across sessions within a test type for this comparison. We first calculated a heterogeneity statistic and examined the results. If the results from this test were not significant (e.g., subjects were homogenous), all subjects' results were pooled for the comparison of initial versus final token preferences.

Results

Social Learning Test

This test examined how a subject's preference for different novel tokens was affected by observing a conspecific partner exchange tokens that were differentially rewarded. The high-value tokens were those rewarded with the more preferred food. The subjects did not show a preference for one token over the other in the initial token preference tests, which measured their token preferences before having watched their partner exchange ($M \pm SE$ of initial preference for designated high-value token = 51.00% $\pm$ 2.77%). Using $p = .51$ as our null hypothesis, we then looked at each individual's choices of the high-value token in the second token-preference test after having watched the conspecific model exchange. Performances by individual monkeys were not significantly heterogeneous, $Gh(7) = 11.41$, $p = .12$, so we were justified in pooling the results across individuals. When pooled, subjects showed a significantly increased preference for the high-

value token in the second token-preference test after watching their partner exchange (see Figure 1), $Gp(1) = 12.12$, $p < .01$.

Nonsocial Transmission Test

This test examined how the subject's preference for different novel tokens was affected by observing one token of a pair being associated with a high-value food item and the other with a low-value food item in the absence of a conspecific partner. This allowed us to determine whether any observational learning required the presence of a conspecific partner or was based on the observation of the stimuli themselves. The subjects did not show a preference for one token over the other in the initial token-preference tests, before they had watched the tokens paired (see Figure 2; $M \pm SE$ of initial preference for designated high-value token = 46.88% ± 3.13%). Using $p = .47$ as our null hypothesis, we found that after observing the tokens paired with their appropriate reward, subjects' choices for the tokens in the second token preference test were significantly heterogeneous, $Gh(7) = 17.30$, $p = .012$. Thus, we were not justified in pooling the data for a group preference. On closer inspection, one individual (an adult female) had developed a significant preference for the low-value token, $G(1) = 17.63$, $p < .01$. No other individual showed a significant preference. If this subject is excluded and the G test repeated, the individuals are not heterogeneous, $Gh(6) = 4.23$, $p = .47$, and these individuals showed no preference for either token when pooled, $Gp(1) = 1.41$, $p = .24$.

Value Reversal Test

In this test, the previously least preferred, low-value token of a familiar pair of tokens was made the high-value item. As expected, the subjects did show an initial preference for the token which had been worth the higher value food in previous exchanges. Thus, the initial preference for the *current* high-value token (former low-value token) was below 50% ($M \pm SE$ of initial preference for designated high-value token = 38.57% ± 7.38%). Using $p = .39$ as our null hypothesis, we found that after having watched their partner exchange this formerly low-value token for a high-value reward, subjects were not heterogeneous in the second token-preference test, $Gh(6) = 10.38$, $p = .11$, and did not show a change
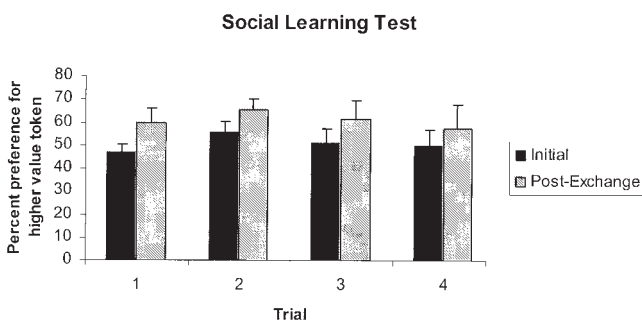

Figure 2. Nonsocial transmission: The mean (±*SEM*) preference of the subjects for the designated high-value token on their first exposure to the token (solid bars) and subsequent to having watched the rewards and tokens paired, without the presence of a conspecific model (hatched bars). This graph includes the female who showed a significant change in preference in favor of the designated low-value reward for the first trial.

in preference toward this now high-value token when pooled (see Figure 3) $Gp(1) = 0.01$, $p = .94$.

Discussion

Capuchin monkeys are able to form a preference for one token out of a pair of novel tokens based on information gained from watching a conspecific model being differentially rewarded for the tokens in a familiar exchange task. The change in preference was highly significant yet modest (i.e., approximately a 20% increase over previous levels), which is not surprising given that the models performed a limited number of exchanges over a relatively short period of time. More extensive exposure to the model or the tokens might have resulted in greater increases in the subjects' preference for one token over the other.

Interestingly, capuchins did not develop the same preference for high-value tokens in the nonsocial transmission test, in which they watched tokens held up with their corresponding reward for the same period of time and in the same location as in the social learning test, but in the absence of a conspecific model. Furthermore, we found that subjects did not show any tendency to learn that new values were attached to familiar tokens. This fits with

Figure 1. Social learning: The mean (±*SEM*) preference of the subjects for the designated high-value token on their first exposure to the token (solid bars) and subsequent to watching a conspecific model exchange the tokens for a reward (hatched bars).
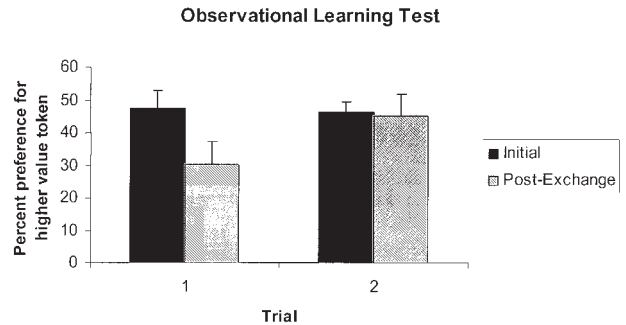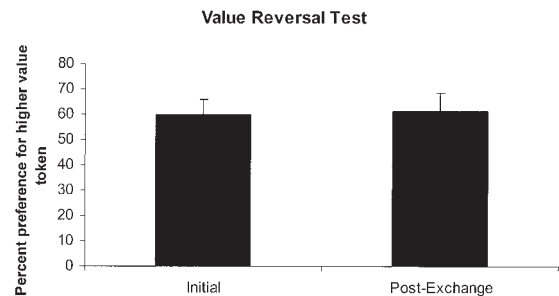

Figure 3. Value reversal: The mean (±*SEM*) preference of the subjects for the designated high-value token on their first exposure to the token and subsequent to watching a conspecific model exchange the tokens for a reward. In this case, tokens were familiar to the capuchins from a previous task in which tokens were associated with the same foods, but the value of the tokens was switched for the current value reversal task.

previous findings that capuchins do not cease consumption of a familiar food that has since been adulterated after watching a group mate reject the food, or even if that group mate becomes ill from consuming the adulterated food item (Visalberghi & Addessi, 2000). Thus, capuchins do learn value in a standard social transmission paradigm but do not learn value in the absence of a conspecific model or when the tokens are not novel. There are several possible explanations for these results.

First, we feel it is unlikely that capuchins can only learn through observation of conspecific actions. Aside from the fact that they did not need to learn an action in this test, they also failed to learn that familiar tokens had changed value, which would have occurred if capuchins learned whatever action they watched a conspecific perform. Second, it is clear that they did not learn from a simple association of tokens, as shown by their performance in the nonsocial transmission test. In this case, the rewards and tokens were shown in the same spatial association as in the social learning test, yet apparently no information was transferred.

Rather, the capuchins seem to need a combination of factors that increase the salience of the available information and thus lead to social transmission. First, it appears that novelty is important for social learning to occur. It is known that chimpanzees only pay attention to a knowledgeable model until a task is mastered (Hirata & Morimura, 2000), and in this case subjects continued paying attention to a familiar task as long as the tokens were novel. Subjects experienced four pairs of novel tokens in their four social learning tests and increased their preference for the more valuable one in every case. However, in the value reversal test, with a familiar pair of tokens, the subjects did not change their preferences for previously familiar tokens, either because familiar tokens attract little attention or because capuchins do not "expect" a need to learn new values. Once values are known, they may never change. In nature, monkeys do not need to deal with changing value (e.g., uncracked nuts always reveal the same meat when opened), so they may not be attuned to obtaining new information about familiar objects.

Second, it appears that the presence of a conspecific increases the salience of the information. In the social learning test, the subject observed a human experimenter manipulating the tokens and rewards and also observed a conspecific consuming the rewards, whereas in the nonsocial transmission tests, the subjects observed only the human experimenter manipulating the tokens and rewards. The difference between the two tests is that subjects did not see a conspecific present or consuming the reward in the second test. Thus, although it is impossible to tell whether the capuchins regard the experimenter as a heterospecific or as a part of their environment, it appears that they needed the extra cue of a conspecific to successfully learn the value of the token. De Waal (2001) has argued that social attachment and identification facilitate social learning, using this as an argument against the use of human models only in animal social learning research and further suggesting an exploration of the social component of social learning. Further proof of the role of conspecifics comes from a recent experiment on the same capuchin monkeys used here, in which the presence of a conspecific affected their response to unequal rewards (Brosnan & de Waal, 2003). On the other hand, the fact that subjects failed to learn new values in the value reversal tests (which did include a conspecific model) indicates that the presence of a conspecific is not sufficient. We feel the most likely expla-

nation for these results is that the presence of a conspecific and of novel tokens combine to enhance attention to reward associations in a way that cannot be achieved by a human model.

The capuchins were surprisingly homogeneous in the nonsocial transmission test, with only one instance of heterogeneity of group response. This was caused by a female who showed a strong change in preference (toward the less valuable token) in one of the sessions. However, she showed no such reaction on the other nonsocial transmission test, which used a different set of novel tokens, nor did any other subject show any change in preference on either set of tokens. Thus, the most likely explanation is that, for some unknown reason, in this isolated case the female formed a preference based on some intrinsic quality of the token that did not have the same effect on other subjects.

The capuchins in our study showed evidence of social transmission, which has been found in few other studies. One possible reason for the success of this task in detecting social transmission may be the paradigm's simple nature. Unlike previous studies, the capuchins did not need to learn a potentially difficult motor task. The individuals needed only to watch a simple task with which they had extensive individual experience (Brosnan & de Waal, in press) to glean information that, from this prior experience, they must know could be useful to them (in the previous test, choosing the high-value token always led to better food). It has been proposed that social learning depends in part on the probability that the model is experiencing the same environment as the subject (Boyd & Richerson, 1988). In our case, the subjects most likely recognized the activity as familiar. Furthermore, the basic information itself did not change (one token from each pair was always worth a Froot Loop, and one was always worth a piece of bell pepper), only the token to which the rewards were matched. Thus, the novel aspect was the tokens themselves, rather than the task or the reward. Perhaps more frequent utilization of familiar and simple tasks will allow us to more fully detect where social learning occurs and how it is useful to the animals who use it as a strategy.

Furthermore, it was impossible for the subjects to gain useful information through direct experience in our study, so they could only learn by observation. For instance, in studies examining the ability of monkeys to socially learn about food items (Addessi & Visalberghi, 2001), it is possible that there exists some exterior cue that could provide information through individual learning, such as the food's odor, texture, or color. These cues, though not providing complete information, may indicate the quality or type of the food item without requiring social transmission of information (Dewar, 2003). This may be particularly true if the novel food shares some characteristic with previously experienced food items (e.g., two types of processed meat products may have similar texture or odor). Because we arbitrarily decided which token would be paired with the higher value reward, there was no cue to indicate which token would be worth the high-value reward; thus, the only way to obtain the information was by watching the external interactions. It is clear that we did not unintentionally create such a cue as the subjects failed to show a preference for one token over the other in the initial token-preference tests. Without external cues informing the subjects about any aspect of the token's value, they had no choice but to learn socially if they wished to gain information about their options.

Even individuals who are capable of social learning may not acquire information socially in all circumstances (Dewar, 2003). In capuchins, both the novelty of the situation and the presence of a conspecific partner appear to contribute to successful social transmission. This finding of social learning skills in the laboratory supports the inference that intergroup behavioral variation in the field represents socially transmitted traditions.

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