

## A Concept of Value during Experimental Exchange in Brown Capuchin Monkeys, *Cebus apella*

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### Key Words

*Cebus apella* · Value perception · Exchange and Barter · Sex differences

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### Abstract

We evaluated the response of brown capuchin monkeys to two differentially valued tokens in an experimental exchange situation akin to a simple barter. Monkeys were given a series of three tests to evaluate their ability to associate tokens with food, then their responses were examined in a barter situation in which tokens were either limited or unlimited. Capuchins did not perform barter in the typical sense, returning the tokens which were associated with the reward. However, females, but not males, showed a different response, preferring the higher-value token. This may indicate that they learned to prefer one token over the other rather than to associate the tokens with their specific rewards. This sex difference parallels previous findings of greater reciprocity in female brown capuchins than in males.

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Animals almost certainly form preferences for items based upon their intrinsic qualities, but the possibility also exists that preferences are based upon qualities extrinsic to the items themselves. In such a case, the animal essentially forms a concept of the value of that item, which may be used to compare different commodities. For instance, such a concept may be used in biological markets, in which dissimilar goods and services are apparently exchanged in a reciprocal fashion [Noë & Hammerstein, 1994, 1995; de Waal, 1997a; de Waal & Berger, 2000; Stopka & Macdonald, 1999].

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We consider this ‘concept of value’ to be short-hand for a reward association with some specific item which can be used in comparison with other items having different reward associations. Thus the value of item x can be weighted against that of y, based upon characteristics extrinsic to both items rather than upon their intrinsic qualities. One way to experimentally demonstrate such a concept of value is to examine whether animals form preferences for inherently non-valuable items based upon their conditioned association with valued rewards. This ability can be tested in a controlled experimental situation in which animals have been trained to exchange material tokens with a human experimenter for a reward.

Non-human primates are excellent subjects for such an exchange task. Chimpanzees exchange items between each other in an experimental setting, both in a contrived situation [Nissen & Crawford, 1936; Savage-Rumbaugh et al., 1978] and spontaneously [Pacquette, 1992]. Several great apes exchange freely with humans as well. Hyatt and Hopkins [1998] found that the majority of chimpanzees, without specific training, would give a non-edible token to a human experimenter in exchange for food. Furthermore, solicitation of the token by the experimenter increased the probability that the chimpanzee would return it, which the authors interpreted as evidence for barter. Chalmeau and Peignot [1998] found that gorillas (*Gorilla gorilla*) were not only capable of simple exchange, but that some of them were able to complete complex exchange interactions in which several items had to be exchanged back before the reward was ultimately received.

We chose to use capuchin monkeys because these primates are known to share material items and food with each other in experimental settings [Thierry et al., 1989; de Waal et al., 1993; de Waal, 1997b, 2000; Westergaard and Suomi, 1997; Westergaard et al., 1998a; Brosnan and de Waal, 2002] and are apparently relatively good at exchange [Westergaard et al., 1998b, 2004]. Capuchins are also known to participate in reciprocal interactions in which donation and receipt of food and/or services are temporally separated, making them likely candidates to possess a concept of value as defined above. Capuchins participate in cooperative interactions in which they must work together to pull in a tray which will reward only one [Mendres and de Waal, 2000; de Waal and Berger, 2000]. Upon receipt of the food, the capuchins share with the individual who helped them obtain it, indicating attitudinal reciprocity [de Waal and Berger, 2000].

Using the same capuchin monkeys as in our cooperation and food sharing studies, we did a series of three studies to evaluate their ability to acquire exchange behavior, then use this behavior in a conditioned association task. We first trained the capuchins on a basic material exchange task, as no other study has documented the acquisition of exchange behavior in this primate. Following this, their response to two inherently non-valuable but differentially conditioned tokens was evaluated in a situation in which subjects were given access to two different tokens and had to return the correct token to the experimenter in order to receive the food reward. We refer to this as the barter task, given that success in the task appears to meet Chapman’s [1980] requirements for ‘pure barter’.

We predicted that capuchins would develop a preference for the higher value token over the lower value token due to the tokens’ associations with differentially valued food items. We further predicted that, after learning to associate the food rewards with the different tokens, the capuchins would be able to successfully obtain food rewards in the barter situation.

## General Methods

### *Subjects*

The subjects included 14 adult and subadult brown capuchin monkeys housed in two social groups at the Yerkes National Primate Research Center, Atlanta, Ga., USA. Only 10 monkeys exchanged consistently enough to participate in testing, 3 adult males, 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.

The groups in which the subjects lived were 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 09.30 h and 17.30 h. A tray consisting of fruit, vegetables and bread with a protein solution was provided to each group every day at approximately 17.30 h. 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 [1997a].

The subjects had previously been trained to enter transport cages, which allowed us to place individual animals into a test chamber with their cooperation. 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, and all testing was carried out in only one of these compartments. The test chamber was backed by an opaque panel, so in the test chamber the subjects had vocal, but no visual or tactile, access to their group. This allowed us to interact with subjects in a controlled manner with minimal distractions from the group. Dependent offspring were always allowed into the test chamber with their mothers.

All but 2 of these individuals had previously been used in food sharing and cooperation studies in our lab. Although this previous experience doubtless made them more sensitive to the possibility of being rewarded for certain tasks, none of their previous experience involved tokens, nor had they been involved in a task in which different items yielded different rewards. As a result, this was their first exposure to experimental value testing and token exchange.

### *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, following Hyatt and Hopkins [1998]. Unless otherwise noted, exchange consisted of the experimenter placing the token(s) into the test chamber, then standing in front of the test chamber with left hand outstretched, palm up, as a begging gesture, and holding the reward above the left hand with the right hand. Subjects received the reward upon the placement of the token into the exchanger's left hand. Attempted exchanges, in which tokens were thrown out of the test chamber or were not placed into the experimenter's hand, were not rewarded. All sessions were videotaped, along with time in hundredths of a second, on either a Super-VHS or digital video recorder and data were later collected from the videotapes by S.F.B. A second observer collected some latency data during testing.

Subjects underwent a number of different experiments, each consisting of some procedure repeated multiple times. Throughout, 'test' refers to an experimental type, 'trial' to the procedure that is repeated multiple times per test, and 'session' will refer to the set of trials for a particular test (i.e. most tests consist of multiple-trial sessions occurring on different days).

### *Statistics*

All statistical tests reported are on a total sample size of 10 individuals, 5 male and 5 female. Analyses of dichotomous preferences for one item over another were conducted using two-tailed binomial tests on data pooled for each subject. In some cases, we also conducted comparisons between two independent groups using the Mann-Whitney U test or

between two dependent groups using the Wilcoxon sign-rank sum test. Since the sample size was below 15, only exact tests were used [Mundry and Fischer, 1998]. All statistics are two-tailed.

## **Experiment 1**

This experiment was designed to ascertain the ability of capuchins to exchange and, after determining their food preferences, to determine whether they could associate tokens with specific rewards.

### *Exchange Training and Acquisition*

Fourteen adults and subadults were initially tested for their ability to exchange. One individual, the alpha male of his group, had had exposure to exchange with humans in his previous laboratory [D. Frigaszy, personal communication] but all other subjects were believed or known to be naïve to the specifics of our procedure. The token initially consisted of a small granite rock (approx. 4 cm in diameter) and the reward was a Kellogg's Apple Jack (a sweet, apple-flavored breakfast cereal approx. 1 cm in diameter). Each session consisted of 20 1-min trials.

Initial training assessed whether monkeys would return the rock spontaneously to an experimenter holding out her hand. For the subjects who did not spontaneously exchange after 5 sessions (i.e. 100 trials), shaping commenced, in which the subject was initially rewarded for throwing the rock out of the test chamber or even for merely touching the rock. Gradually, the stringency of the criteria increased until the subject exchanged correctly.

After task acquisition, five baseline test sessions (BL) were run to establish the standard latency to exchange, which was defined as the number of seconds it took the subject to return the token to the experimenter's hand after the token had been placed in the chamber. The session in which the subject first successfully exchanged in 90% of the trials was counted as the first BL session. For each BL trial, the latency to exchange and the errors made (e.g. throwing the item out of the test chamber) were recorded, as well as ad libitum data on social behaviors aimed at the human exchanger. At least two experimenters played this exchanger role in different BL sessions to assure that the subjects generalized exchange across multiple persons (although all testing was completed by S.F.B.). If a subject failed more than 10% of trials during any single BL session, training recommenced.

### *Conditioning Procedure*

This task was designed to teach the capuchins the value of two different, inherently non-valuable tokens. The procedure was intended to condition subjects that two different tokens were worth two different food items (one of which was more valuable than the other). The tokens used in the conditioning procedure were a small polyvinyl chloride (PVC) pipe and a large metal washer. The capuchins did not show an initial preference for either of these tokens, nor for either of 4 other pairs of tokens tested [Brosnan and de Waal, unpublished data]. Since there was no initial preference for either token, and we planned to use these value associations in future testing, for all subjects the PVC pipe (pipe) was associated with a piece of fresh bell pepper and the metal washer (washer) was associated with a Froot Loop.

These food items had previously been established as the lowest (bell pepper) and highest (Froot Loop) value food items for all 10 capuchin subjects (see Food Preference Test below).

Prior to the first conditioning test, the subjects were exposed to 5 of each token for 30 min to reduce their novelty. For each trial, 5 of each of the two tokens were placed on the floor of the test chamber (for a total of 10 items) simultaneously. The subjects could exchange the tokens back in any order they chose. Each returned token was rewarded appropriately by the experimenter. The food reward was handed to the subject immediately upon return of a token and, typically, an exchange took about 5 s from the subject picking up a token to receiving the food reward. Each subject received 2 sessions with 5 trials per session, for a total of 50 exchanges with each token.

#### *Food Preference Test*

This test established food preferences for each individual in the manner of de Waal [1997b]. The subject had to make a choice between two simultaneously offered food items, of which it could obtain only one. The experimenter held the foods in different hands in front of the subject, separated by approximately 10 cm. The subject was allowed to reach through the mesh of the test chamber and take only 1 of the food items. Ten choices were offered between each possible pair of foods, split between 2 different sessions. Reward position was alternated randomly, but with an equal number on each side. It was noted from which side the item was obtained to ensure that no subject simply preferred the item from one side to that from the other. The trials were run in quick succession, with each new pair of foods being offered when the previous choice was consumed.

Each individual's preferences were established across 5 different foods, a Kellogg's Froot Loop (a sugary, fruit-flavored breakfast cereal), a 500-mg Noyes precision food pellet (sucrose pellets), a green bell pepper piece, an apple piece, and a cucumber piece. All fruit or vegetable pieces were approximately 2 cm in diameter. A reward was considered to be preferred if the subject chose it at least 80% of the time over the alternative.

#### *Token Preference Test*

The purpose of this test was to see if the subjects would recognize the value of inherently non-valuable tokens based on previous conditioning. The procedure was the same as the Food Preference Test, except the choice was made between two tokens instead of two items of food. Ten choices were offered per session, at the end of which the subjects received a single peanut to maintain their motivation to cooperate. Each subject received 5 test sessions, hence 50 trials. These data were used to ascertain that a preference had been established during the conditioning procedure. All subjects were used in subsequent tests, regardless of whether they demonstrated a preference for one token over another, as we had no way of knowing whether they failed to demonstrate a preference because they lacked a concept of value or because they lacked motivation to participate in the preference test. Specifically, it seemed possible that due to motivational or some other environmental differences, a subject might fail to demonstrate a preference in this test but do so in subsequent experiments. Only one male failed to show a preference in the token preference test (see Results).

## *Results*

### *Acquisition*

Twelve of the initial 14 individuals successfully learned the exchange task (2 adult females did not learn to exchange in 25 sessions). Of these, 10 learned to exchange with no shaping (that is, within 5 sessions) and 2 adult females required extensive shaping (15 or more sessions). Of the 10 that learned with no shaping initially, 2 subadult males ceased exchanging consistently for unknown reasons (most likely social stress) and were not included in subsequent tests. This left only 10 subjects, 5 adult males and 5 adult females, for all following tests. As there were no differences in behavior between the 8 subjects who required no shaping and the 2 subjects who did require shaping, their results are lumped for all subsequent analysis.

### *Food Preferences*

All 10 subjects preferred Froot Loops over bell pepper (mean  $\pm$  SEM preference for Froot Loop of  $95.00 \pm 2.69\%$ , binomial test:  $p < 0.001$ ). There was no sex difference in preference for the Froot Loop (mean  $\pm$  SEM preference for females of  $98.00 \pm 2.00\%$  compared to preference for males of  $92.00 \pm 4.90\%$ ; Mann-Whitney:  $U = 9$ ,  $n = 10$ ,  $p = 1.00$ ).

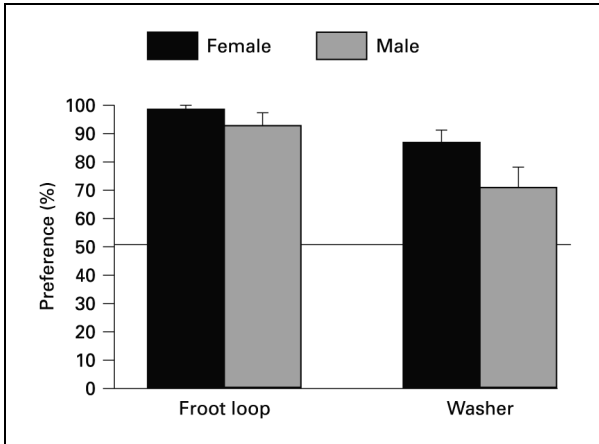
### *Token Preference Test*

Nine out of 10 subjects chose the more valuable washer more often than they chose the pipe, and the exceptional subject chose each token equally often (mean  $\pm$  SEM preference for washer of  $78.40 \pm 4.93\%$ ; binomial test:  $p < 0.001$ ). To see whether preference for the higher-value reward differed in strength from preference for its corresponding token, the percentage of washers chosen (over pipe) for each individual was compared with the percentage of Froot Loops chosen (over bell pepper). The preference for the token was weaker than for the reward (fig. 1; Wilcoxon:  $T = 45$ ,  $n = 9$ ,  $p < 0.001$ ). There was no difference between males and females in their preference for the washer (Mann-Whitney:  $U = 6$ ,  $n = 10$ ,  $p = 0.222$ ).

## *Discussion*

Capuchin monkeys can be taught to exchange material items with a human experimenter, thus this behavior can be used to investigate the monkeys' perception of value. Material exchange is not necessarily a spontaneous behavior in capuchin monkeys, but it is rapidly acquired by a majority of individuals and can be learned by most of the rest. There is no difference in responses to later tests for individuals who exchanged spontaneously versus those who required extensive shaping. Capuchins seem less inclined to material exchange than great apes, as captive chimpanzees require even less experience to acquire the task [S. Brosnan, pers. observation].

As predicted, capuchins form preferences for inherently non-valuable tokens based on the association of these tokens with different rewards. The subjects learned to prefer the washer, the high-value token worth a Froot Loop, to the pipe, the low-value token worth a bell pepper piece, apparently based on their preference



**Fig. 1.** The capuchins' preferences for the higher-value food (Froot Loop) as compared to their preference for the higher-value token (washer), which was the token associated with the Froot Loop. The capuchins preferred the higher value over the lower value for both food and tokens, although the token preference was less strong than the food preference. There was no sex difference in preference for either the food or the token. The line at 50% represents preferences expected by chance.

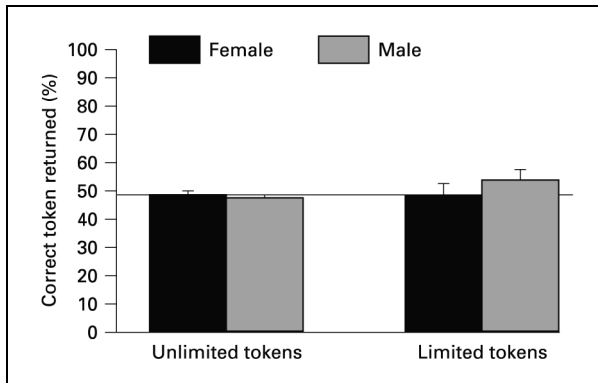
for the Froot Loop. The strength of the preference for the food reward itself was greater than the strength of preference for the corresponding token, which might be expected, given that the food reward has intrinsic value and the token only associated value.

## Experiment 2

As the previous experiment indicated that capuchin monkeys are easily able to associate food rewards with inherently non-valuable tokens, we next examined whether they would be able to return the correct token to receive a proffered reward in a task akin to a simple barter situation. This and the following experiment were designed to ascertain how the conditioned value affected the subjects' exchange behavior.

### *Value Association Test, Unlimited Tokens*

For this test, the subject had to return the token that was associated with a proffered reward in order to receive the reward. The experimenter began by holding the reward in front of the subject, to make the subject aware of it. Following this, the two different tokens were placed on a table in front of the subject, approximately 4 cm from the test chamber and 16 cm apart. The exchanger placed her open left hand (receiving hand) directly between the tokens (each was ~2 cm from her hand), then held the reward in her right hand, directly over her outstretched left hand. The subject could choose and return either of the tokens.



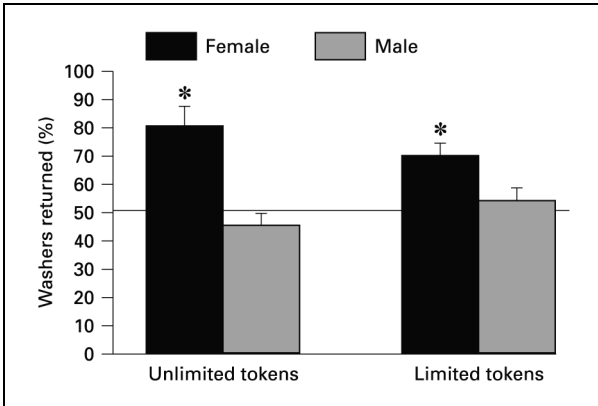
**Fig. 2.** The percentage of tokens returned correctly (that is, tokens returned that were associated with the proffered reward) in the unlimited barter situation, in which 1 of each token was available for each exchange, and the limited barter situation, in which the number of tokens was set at the commencement of the trial. The line at 50% represents the percentage of correctly returned tokens expected by chance alone. The subjects did not return the tokens that were associated with the proffered reward.

Once again, the tokens were a washer and a PVC pipe. The washer was the higher-value of the tokens, worth a Froot Loop, and the PVC pipe was the lower value, worth a piece of bell pepper. The subjects only received the reward if the correct token (e.g. the one that was associated with the proffered reward) was returned. The position of the tokens was alternated each trial and the order of presentation of rewards was random, but with an equal number of both rewards during each session. If the subject failed to return either item after 25 s, the tokens were removed and the next trial commenced. In situations in which the subject maintained possession of a token at the end of the trial, 1 of each token was still made available for the next trial, to assure the subject knew they had access to at least 1 of each token. Each session consisted of 25 trials and each subject received 4 sessions.

### *Results*

The number of correct returns was calculated for each individual as those responses in which the token returned was associated with the proffered reward. For this test, the subject had access to 1 of each token for each trial (exchange). Since for each exchange the subjects always had access to 1 of each token, in each trial the subjects had a 50% chance of returning the correct token. Subjects did not return the tokens correctly (fig. 2: mean  $\pm$  SEM of  $47.8 \pm 0.75\%$  for correct token; binomial test:  $p = 0.851$ ), and there was no sex difference (female mean  $\pm$  SEM of  $50.9 \pm 1.09\%$ ; male mean  $\pm$  SEM of  $53.8 \pm 1.68\%$  for correct returns; Mann-Whitney:  $U = 6$ ,  $n = 10$ ,  $p = 0.222$ ).





**Fig. 3.** The percentage of washers returned in the unlimited barter situation, in which 1 of each token was available for each exchange, and the limited barter situation, in which the number of tokens was set at the commencement of the trial. For the limited situation, the percentages on the Y-axis indicate the percentage of washers returned in the first 5 (that is, the first half) of exchange sessions. The line at 50% represents the percentage of returned washers expected by chance alone for both the unlimited and limited token scenarios. There is a strong sex difference, with males returning washers at chance levels only and females returning washers at higher than chance levels (indicated by asterisk), supporting the Value Maximization hypothesis.

However, the capuchins as a whole did show a preference for the higher-value token (mean  $\pm$  SEM of  $62.42 \pm 7.07\%$ ; binomial test:  $p < 0.001$ ). Upon further analysis we realized this was due to a sex difference (fig. 3: Mann-Whitney:  $U = 1$ ,  $n = 10$ ,  $p = 0.016$ ), with female capuchins being more likely to return the high-value token than the lower-value token (female mean  $\pm$  SEM of  $79.9 \pm 7.15\%$ , binomial test:  $p < 0.001$ ), while males were, if anything, more likely to return the lower-value token (male mean  $\pm$  SEM of  $44.9 \pm 4.54\%$ , binomial test:  $p = 0.031$ ). The females did not return the higher-value washer significantly more often when the Froot Loop was offered than when the bell pepper was (Froot Loop offered mean  $\pm$  SEM of  $40.4 \pm 3.27$ ; bell pepper offered mean  $\pm$  SEM of  $36.6 \pm 4.13$ ; Wilcoxon:  $T = 10$ ,  $n = 4$ ,  $p = 0.125$ ).

### Discussion

As opposed to our initial predictions, capuchins did not return the tokens that were associated with the proffered rewards. However, the females showed a strong preference for returning tokens worth the higher-value food regardless of what reward was being offered. This presented two challenges: first, to describe the strategy the females were apparently following, and second, to understand the sex difference in responses. The sex difference is addressed later in the General Discussion.

We realized that the capuchins could follow two different strategies to obtain the rewards. First, subjects may return the 'correct' token, or the token which is associated with the proffered reward, attempting to maximize the overall number of rewards earned, which we dubbed the 'Matching' strategy. This was the strategy we initially predicted, but it was not followed in this situation. This strategy seems cognitively quite demanding, requiring the subject to know that the tokens have different values, to remember these values, and to associate the tokens with the proffered reward (which also must be recognized).

Second, subjects may return only the highest value tokens, which we call the 'High Value' strategy. While this strategy is inferior in terms of achieving rewards, it may be superior in that it allows for the maximum receipt of high-value rewards with minimum effort. The subjects need not pay attention to the proffered reward or remember the values of the tokens, but must only recognize which token will acquire their preferred food. This is similar to the females' behavior in this test.

There were several possible explanations for this preference for the higher-value token. First, it is possible that the capuchins do not understand the task, and the statistically significant preference for the higher-value token by the females was a fluke. Further testing will shed light on this possibility. Second, perhaps the capuchin females do show a robust preference for returning the higher-value token, following the High Value strategy. However, while this may require the least attention for the best rewards, it seems unlikely that the capuchins cannot make the conditional association required for the Matching strategy. This leads to the third possibility, that the capuchins can perform the conditional association, but are not in a situation in which it is beneficial. In this experimental situation, in which tokens are unlimited, the capuchins could receive all of the higher-value rewards by following this High Value strategy. As none of our animals are food deprived, the lower value foods may not have been sufficiently motivating. The third experiment was developed as a way to encourage the capuchins to maximize their performance without food deprivation.

### **Experiment 3**

This task was designed to determine if capuchins will spontaneously make conditional associations, using tokens whose associated values are already familiar, if they are in a situation in which they must pay attention to maximize receipt of higher-value rewards. To this end, we designed a limited token situation to minimize the gains of indiscriminately returning the higher-value token. In the prior experiment, subjects had access to 1 of each token prior to every exchange. In this 'limited' task, a set number of tokens was given to the subjects prior to a series of exchanges, while allowing the subjects to see the order in which rewards would be offered. Thus, subjects who know which token is associated with which reward should attempt to maximize high-value rewards by returning the correct token, while those who only know that 1 token is superior to the other should continue to show a preference for the higher-value token. This test was completed on all 10 subjects to see if the males responded in a different manner to this different situation.

### *Value Association Test, Unlimited Tokens*

The procedure for this test was similar to that of the unlimited test, except that the tokens were now a limited resource. Five of each token were placed with the monkey in its test chamber at the commencement of the session, rather than giving the subject guaranteed access to 1 of each token per trial. This meant that subjects depleted their supply of tokens as they exchanged, and these tokens were not replaced. As a result, subjects could run out of either of the token types before all of the associated rewards had been offered. Sessions consisted of 10 trials (5 of each reward type placed with the monkey) and each subject received 5 sessions for a total of 50 trials.

### *Results*

The number of correct returns was calculated per subject in the same manner as above. Subjects did not return the correct token (the one that was associated with the reward) more than the incorrect one (fig. 2: mean  $\pm$  SEM of  $50.54 \pm 2.97\%$  for correct token; binomial test:  $p = 0.099$ ), and there was no sex difference in whether or not the correct token was returned (female mean  $\pm$  SEM of  $48.08 \pm 4.18\%$ ; male mean  $\pm$  SEM of  $53.00 \pm 4.37\%$ ; Mann-Whitney:  $U = 8$ ,  $n = 10$ ,  $p = 0.421$ ).

For this test, measurement of a subject's preference for a token was more complex. Since the subject was given 5 of each token prior to the commencement of the session and these tokens were not replenished during the session, there was no guarantee that 1 of each token would be available for each trial, and the probability of returning any 1 token was different for each trial, dependent upon previous returns. Thus we calculated which tokens they chose to return first in the trials as a proxy for the preferred token. To do this, we calculated the frequency of high-value tokens returned in the first half of exchanges, that is, how many high-value tokens they chose to return in the first 5 exchanges in each series of 10 exchanges. In this case, subjects showed a preference for returning first the higher-value token, the washer (mean  $\pm$  SEM of  $3.1 \pm 0.22$ , binomial test:  $p < 0.001$ ); however, once again this result is due to a sex difference (fig. 3: Mann-Whitney:  $U = 3.5$ ,  $n = 10$ ,  $p = 0.056$ ), with females showing a strong preference for higher-value tokens (female mean  $\pm$  SEM of  $3.5 \pm 0.26$  washers returned in the first half, binomial test:  $p < 0.001$ ) and males showing no preference (males: mean  $\pm$  SEM of  $2.72 \pm 0.27$  washers returned in the first half, binomial test:  $p = 1.00$ ).

### *Discussion*

Once again, there is no evidence that the capuchins are following the Matching strategy, in which they return the token associated with the proffered reward. However, again the females, but not the males, preferred to return the higher-value token. In this limited situation, the females are more likely to return the higher-value tokens first, indicating a preference for them. Thus, this test provides more support for the conclusion that capuchin females are following the High Value strategy.

## General Discussion

Overall, capuchins failed to return the correct token regardless of whether their access to tokens was unlimited or limited. So, capuchin exchange behavior does not support the Matching strategy, in which subjects maximize the overall number of rewards received. If our assumptions of what the capuchins must know are correct, evidently the capuchins did not have the cognitive capacity to retain these two value assessments and relate them to the offered reward.

It is, to us, somewhat surprising that the capuchins cannot do this conditional association task. There are several possibilities for why this may be. First, even in the limited task, the capuchins may not be in a situation which drives them to use all of their abilities to obtain food. These are captive individuals who have ad libitum access to food and water and receive fruits and vegetables daily. Thus, food may not be in sufficiently short supply to be motivating. These results might be different in the case of more deprived individuals (e.g. those living in the wild). Second, it may be that the capuchins could learn this task if subjected to a longer period of training and conditioning, but that their natural first response is not to match the tokens and rewards. Finally, it may be that the capuchins do not possess the cognitive sophistication which will allow them to perform such a task.

However, among the females, a preference for returning the higher-value token is consistent across 2 sets of tests separated in time, indicating the High Value strategy. Apparently, the capuchin females have not learned 2 value associations (e.g. washer = Froot Loop and pipe = bell pepper) but instead have learned a single value association (washer > pipe) and use this to complete the task. If our assumptions about what the capuchins must know or understand in order to follow the High Value strategy are correct, these females probably do not consider the explicit worth of each token but, instead, learn only to prefer the washer to the pipe. Thus they return the washer more frequently.

There are several alternative explanations for the females' behavior that we cannot completely rule out. First, it may be that the capuchins are confusing this task with the earlier token preference tests, and hence are simply demonstrating their preference for the higher-value token. However, the capuchins have been subjected to food preference tests for years with no confusion, the token preference tests and the value association tasks were separated in time by several days, and the tasks were set up in a different fashion. Moreover, the fact that this 'confusion' occurs among the females, but not the males, seems unlikely. Another possibility is that the capuchin females may be 'asking' for the higher-value food, that is, returning the token that matches the food they *desire* rather than the food that is being offered. Finally, they may understand the action as barter, but they are uninterested in the lower-value rewards to the point of ignoring them. Such behavior would create a similar response. This last possibility could best be distinguished by using food-deprived individuals.

### *Capuchin Sex Difference*

In this test, both males and females showed an equal preference for the higher-value token in the Token Preference Test, but only females showed non-random responses to the barter situation. Thus the sex difference is in the utilization of preferences, rather than the ability to form preferences per se. This sex difference is

somewhat surprising, but in line with some previous research. While, obviously, comments on the basis of such a small sample size are speculative, the consistency with which we found these results merits further attention.

One possibility is that there was some mechanical difference between the males and the females that rendered the sex difference likely (e.g. perhaps the males were less inclined to pick up washers from a flat surface). While this is always possible, the relatively small degree of sexual dimorphism in this species leads us to believe it is unlikely. We believe this result may be related to sex differences in reciprocal behavior found previously in brown capuchins.

Several independent lines of evidence indicate that female brown capuchin monkeys are more reciprocal than males [de Waal, 1997a; di Bitetti, 1997]. In field situations, females allogroom more reciprocally than males [di Bitetti, 1997]. In experimental situations, capuchin males share indiscriminately with almost all partners, regardless of return benefits, whereas capuchin females share on a reciprocal basis, meaning that there is a contingency between give and take [de Waal, 1997a]. It has been hypothesized that this different attitude to sharing and exchange may have evolved owing to different reproductive strategies and societal pressures on males and females. Adult male capuchins residing within a social group may increase their fitness by sharing indiscriminately with females and juveniles in the group, as they are potentially the fathers of current and future juveniles. On the other hand, females are reproductively vested only in themselves and their offspring and can most increase their fitness by restricting sharing to their own offspring and close female allies with whom they have a reciprocal relationship [de Waal, 1997a].

If a similar principle is involved in this material exchange task, this difference between a paternal investment strategy by males and reciprocity by females may make females more attuned than males to value in reciprocal interactions. For males, this tendency to interact outside of reciprocal relationships may lead to them paying less attention in our exchange task. Although they are as likely as females to prefer the higher-value token to the lower-value one, they do not show a barter strategy which reflects these preferences. Among females, their tendency to maintain reciprocal relationships may make them more likely to follow some strategy during our material exchange task. Although they fail to follow the strategy to maximize their receipt of rewards, they do show a strong preference for high value tokens, returning them regardless of the reward offered.

## **Acknowledgments**

This research was made possible by a grant IBN-0077706 from the National Science Foundation to the senior author, an NSF Graduate Research Fellowship to the first author, and the NIH basegrant (RR-00165) to the Yerkes National Primate Research Center. We are grateful to Laura Mullen, Lisa Bradley, and Jason Davis for assistance with testing and data collection. We also thank the animal care and veterinary staff for maintaining the health of our study subjects. Finally, we thank Kate Baker, Julian Bragg, Bill Hopkins and Harold Gouzoules for helpful discussion and several anonymous reviewers for helpful comments on an earlier draft of the manuscript. The Yerkes Primate Center is fully accredited by the American Association for Accreditation of Laboratory Animal Care.

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