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Responses to a simple barter task in chimpanzees, *Pan troglodytes*

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Abstract Chimpanzees (*Pan troglodytes*) frequently participate in social exchange involving multiple goods and services of variable value, yet they have not been tested in a formalized situation to see whether they can barter using multiple tokens and rewards. We set up a simple barter economy with two tokens and two associated rewards and tested chimpanzees on their ability to obtain rewards by returning the matching token in situations in which their access to tokens was unlimited or limited. Chimpanzees easily learned to associate value with the tokens, as expected, and did barter, but followed a simple strategy of favoring the higher-value token, regardless of the reward proffered, instead of a more complex but more effective strategy of returning the token that matched the reward. This response is similar to that shown by capuchin monkeys in our previous study. We speculate that this response, while not ideal, may be sufficient to allow for stability of the social exchange system in these primates, and that the importance of social barter to both species may have led to this convergence of strategies.

Keywords Barter · Chimpanzees · Exchange · Tokens

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Introduction

Although it has been demonstrated that chimpanzees (*Pan troglodytes*) can use tokens as secondary rewards, i.e. relate the value of a food reward to a token and respond similarly to both the token and food reward (Cowles 1937; Sousa and Matsuzawa 2001; Wolfe 1936), it is unclear if chimpanzees can use token-associated values in a primitive economy to “barter” for rewards. We previously determined that capuchin monkeys (*Cebus apella*) are capable of such barter (Brosnan and de Waal 2004), and we here report data for a similar experiment with chimpanzees.

Whether or not chimpanzees can barter has interesting implications for their social interactions. Chimpanzees exchange goods and services, such as food (de Waal 1989) or coalition support (de Waal 1982), as well as dissimilar commodities, such as grooming for food (de Waal 1997a). To be most effective as a long-term strategy, individuals should be able to judge, at least relatively, the return investment required of them, or they may lose out to individuals who cheat by shirking rather than omission (Packer 1988). One difficulty in judging individual investment in exchange is that it is hard to compare the value of different goods and services to different individuals (Boyd 1992; Seyfarth and Cheney 1988). With this in mind, we created a multi-token exchange in a controlled laboratory situation to determine whether or not chimpanzees are capable of judging the return necessary to receive some benefit in a very simple barter situation.

Our experiment is based upon an exchange paradigm. This paradigm was previously used successfully with capuchin monkeys (Brosnan and de Waal 2004), and we expected chimpanzees to be even more adept at exchange. Chimpanzees are known to exchange items between each other in an experimental setting, both in a contrived situation (Hyatt and Hopkins 1998; Nissen and Crawford 1936; Savage-Rumbaugh et al. 1978) and spontaneously (Paquette 1992). Great apes, including

chimpanzees, exchange freely with humans as well (Hyatt and Hopkins 1998). Hyatt and Hopkins (1998) found that chimpanzees would easily give a non-edible token to the experimenter in return for a food reward. Furthermore, solicitation of the token by the experimenter increased the likelihood of the chimpanzee returning it, which the authors took as evidence of primitive barter.

For the present study, chimpanzees could exchange one of two tokens for its associated reward. Thus, subjects had the opportunity to return either token, but only by returning the correct token could they receive their reward. Chimpanzees' concept of the value of the token may evidence itself in one of two ways during the bartering test. First, subjects may return the 'correct' token, or the token that matches the proffered reward, attempting to maximize the overall number of rewards earned. We call this the *matching* strategy. This strategy assumes that chimpanzees recognize the specific associations for each token/reward pair and know to return the token that matches the proffered reward in order to receive the reward. This seems cognitively quite demanding, requiring the subject to not only remember the reward-associations of multiple tokens, but to monitor the proffered reward and match it to the correct token.

Second, subjects may return only the highest value tokens, attempting to maximize their receipt of high-value rewards at the expense of lower-value rewards. We call this the *high value* strategy. This strategy can come about in two different ways. First, subjects may not be interested in the lower-value reward and do not care whether or not they receive it, and so attempt to maximize receipt of high-value rewards by always returning the higher-value token. Second, subjects may not be capable of remembering such complex information as which token corresponds with which reward, but do remember that one token brings in superior rewards to another and so learn only to prefer that token worth the higher-value reward, without remembering explicit token/reward associations. This is cognitively simpler than the matching strategy as the subject need only remember one value association (high-value token > low-value token) and need not monitor the proffered reward, nor attempt to match it to the correct token.

To distinguish between these possibilities, we designed both limited token and unlimited token situations. In the unlimited token task, subjects have access to one of each token prior to every exchange. In the limited token task, a set number of tokens is given to the subjects prior to a series of exchanges, while allowing the subjects to see the order in which rewards will be offered. In the unlimited situation, it may be impossible to distinguish between the two methods of arriving at the high value strategy, as subjects may be uninterested in low-value rewards, and hence only return high-value tokens (perhaps "asking" for a superior reward, or because it requires less effort), or may only remember the one association, leading them to return high-value

tokens (their favorite) preferentially. In the limited situation, however, subjects who want to maximize receipt of high-value rewards must return the correct token (since token access is limited, they will run out of high-value tokens before high-value rewards are all achieved), so they should show the matching strategy, while those who only know that one token is superior to the other should continue to show the high value strategy. This allows us to distinguish between our two competing hypotheses.

In the earlier study, we found that capuchins quickly learn to prefer the token worth the higher-value reward over the one worth the lower-value reward (Brosnan and de Waal 2004). Their preference for the token worth the higher-value food was not as strong as their preference for the higher-value food itself (as compared to the lower-value food), probably reflecting the fact that the tokens only *represented* food and so elicited a less strong response. Furthermore, female, but not male, capuchins followed the high value strategy, showing a preference for returning higher-value tokens preferentially regardless of the reward being offered. This was true in both the limited and unlimited situations. Males, although they formed a preference for the high-value token initially, returned tokens randomly in both barter situations. We attribute this to a known tendency for female capuchins to interact reciprocally while males interact more indiscriminately (de Waal 1997b; di Bitetti 1997). This is proposed to be due to features of their social ecology which encourage male investment in all group members, but female investment only in offspring and a few other adult females (de Waal 1997b). Unfortunately we were unable to statistically evaluate any sex differences in chimpanzees as too few males participated in the study.

Based on our capuchin study and previous exchange and token studies using chimpanzees, we expected that chimpanzees would have no difficulty forming a preference for the higher-value token after being conditioned in a similar regimen to the capuchins. We further predicted that the chimpanzees might demonstrate the cognitively more demanding matching strategy.

Methods

Subjects

The chimpanzees used were 9 individuals from a group of 17 housed at the Yerkes National Primate Research Center Field Station, Lawrenceville, GA, USA. The apes consisted of 1 adult male, 7 adult females, and 1 sub-adult female. Individuals were tested separately, with the exception of 2 females who brought their dependent offspring into the testing area with them.

These individuals were housed in a large outdoor corral, to which is attached a series of indoor runs connected by pneumatic doors. The chimpanzees had *ad libitum* access to water and were fed Purina primate

chow three times per day at approximately 0800, 1200, and 1700 hours. Fruits and vegetables were distributed with the last feeding of the day. No animal was ever food or water deprived for any of these tests, so motivation depended upon their interest in the task and the rewards. The chimpanzees were tested in the indoor runs that were part of their day-to-day quarters. The chimpanzees were called into the runs when we were ready to test and were only tested if they appeared. As a result, testing was on a strictly voluntary basis. There were several other adult male chimpanzees who came in occasionally, but their data were excluded as they did not consistently volunteer for testing and hence full data sets were not collected.

None of the individuals used for this test needed to be trained to exchange; all of them spontaneously began to exchange upon receipt of the token. We ran two series of 20 exchanges with each subject over 2 days to verify their consistency in the behavior and get them accustomed to exchanging in a structured situation.

Food preference test

Prior to conditioning, we established the chimpanzees' relative preferences for different food items. This test established food preferences for each individual in the manner of de Waal (1997b). Food preference was determined by holding up one piece of each of two foods in front of the chimpanzee. They were allowed to choose one, and the one they chose was considered to be their favorite. Preference was defined as a subject showing 90% or greater preference over a series of ten trials.

Foods tested for preference included seedless grapes, thin slices (approximately 5 mm) of banana, apple pieces and yellow squash pieces (both approximately 15×10×5 mm). Ultimately, we used seedless grapes as the high-value food and yellow squash pieces as the low-value food.

Conditioning procedure

Conditioning was done by associating one of a pair of tokens with the high-value food and one of the same pair of tokens with a low-value food. Tokens in this case were polyvinyl chloride (PVC) tubes of different length, color, and pattern. Three distinguishing features were used to assure that all chimpanzees could tell the tubes apart. The token associated with the high-value food was a long (20 cm) tube painted in a "candy-cane" pattern of alternating red and white stripes. The token associated with the low-value food was a shorter (14 cm) tube painted solid black.

To condition the subjects, three of each tube were placed in the run with the chimpanzee, and they were allowed to return them in any order they wished. As they returned tokens, the reward that matched the returned token was given to them. Subjects received four sessions

over a series of 4 days. Each session had seven series of 6 exchanges (3 each with the high and low-value tokens) for a total of 84 exchanges with each token for each chimpanzee.

Token preference test

Both prior to and immediately following conditioning, a token preference test was done to ascertain what preference the subjects had for each token. Token preference tests were done in the same manner as the food preference tests; one of each token was held up before the chimpanzee and the token they chose was considered to be their preferred token. Each token preference test consisted of a series of 20 choices. After every 10 choices, the tubes were hidden and subjects were given an unrelated food reward (typically a piece of banana) to keep them motivated to participate.

These tests had a twofold purpose. Initially, they were used to demonstrate that the subjects did not initially prefer one token to the other. Following the conditioning trials, they were used to demonstrate that the subjects had formed a preference for one of the tokens, presumably based upon the conditioning. 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.

Unlimited barter test

This test and the following test were designed to ascertain how the conditioned value of the tokens affected the subjects' exchange behavior. The subject had to return the token that matched 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, one of each token was placed through the mesh in the front of the run, approximately 6 cm apart. The chimpanzee was allowed to choose one of the tokens and take it into the run. If they took both simultaneously, they were allowed to keep them. Following this, the exchanger placed her left hand at chest level on the chimpanzee, directly in front of the chimpanzee, in the stereotyped exchange gesture. The subject could then return the token to the experimenter.

Once again, the tokens were a long red striped tube (red token) and a short solid black tube (black token). The red token was the higher-value of the tokens, worth a grape, and the black token was the lower-value of the two, worth a piece of yellow squash. The subjects only received the reward if the correct token (that which matched 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 each session. In situations in which the subject maintained possession of a token at the end of the trial, one of each token was still made available for the next trial, to assure the subject knew that they had access to at least one of each token. Each session consisted of 20 trials and each subject received two sessions.

Limited barter test

The procedure for this test was similar to that of the unlimited token test, except that the tokens were now a limited resource. Three of each token were placed in the run with the chimpanzee at the commencement of each exchange session, rather than giving the subject guaranteed access to one 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. Each session consisted of eight trials of 6 exchanges (3 for each reward) and each subject received one session for a total of 48 exchanges. This test followed the unlimited paradigm, as we expected this test to be more difficult for the chimpanzees.

Statistics

We tested the null hypotheses that the chimpanzees' responses were greater than 50% (chance) using exact Wilcoxon Signed-Ranks tests for location (Daniel 1995). We also conducted comparisons between two dependent groups using the Wilcoxon Signed-Ranks test. Since the sample size was below 15, only exact tests were used (cf. Mundry and Fischer 1998). Finally, in the species comparisons, we used univariate Analysis of Variance (ANOVA) tests to distinguish between the responses of chimpanzees, capuchin females, and capuchin males. All statistics are two-tailed.

Results

Food preference test

Chimpanzees showed a strong preference for grapes over squash, choosing grapes the majority of the time (mean \pm SEM for grapes = $96.67 \pm 1.67\%$, $T=0$, $n=9$, $P=0.004$). Six of nine subjects chose the grape 100% of the time, while the remaining three subjects preferred the grape 90% of the time.

Token preference test

Chimpanzees developed a preference for the long, red striped token which was associated with the grape over

the short, black token associated with the squash (Fig. 1: mean \pm SEM for high-value token = $71.91 \pm 5.70\%$, $T=0$, $n=9$, $P=0.004$). To see if preference for the higher-value token differed in strength from preference for its corresponding reward, the percentage of red tokens chosen (over the lower-value black tokens) for each individual was compared with the percentage of the higher-value food, grapes, chosen (over the lower-value food, squash). Chimpanzees show a stronger preference for the higher-valued food item than its corresponding higher-value token (Wilcoxon Signed-Rank Test, $T=42.5$, $n=9$, $P=0.0196$), which is expected given that the food item has inherent value while the token has only associated value.

Unlimited barter situation

This test measured which of the tokens (the low-value black token or the high-value red striped token) the chimpanzees preferred to return when offered either of the rewards (the high-value grape or the low-value squash). In this situation, chimpanzees were not limited in their access to tokens, that is they had access to one of each token for each trial (exchange). The number of correct returns was calculated for each individual as those responses in which the token returned matched the proffered reward. Since for each exchange the subjects had access to one of each token, in each trial the random expectation of subjects returning the correct token was 50%. Subjects showed a slight preference for returning the correct token, that is the one that matched the

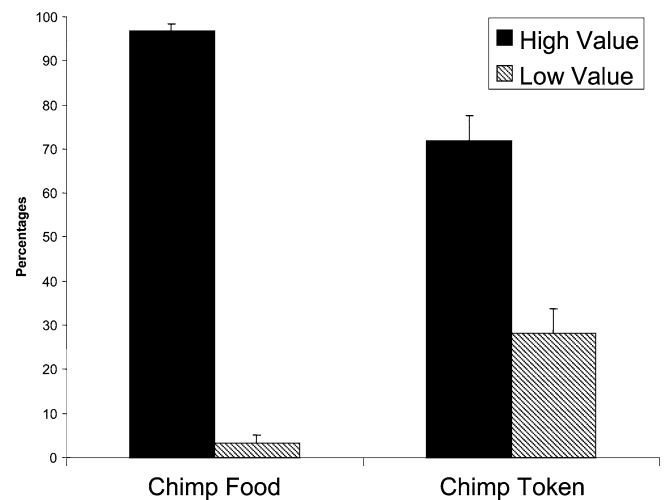


Fig. 1 Chimpanzees (*Pan troglodytes*) show a strong preference for grapes, the high-value food (solid bar) over yellow squash pieces, the low-value food (hatched bar) and a corresponding preference for the high-value token (solid bar), conditioned to be worth the high-value food, over the low-value token (hatched bar), conditioned to be worth the low-value food. Furthermore, the chimpanzees' preference for the high-value food is stronger than their preference for the high-value token. This is expected, as the value of the tokens is associated rather than inherent

proffered reward, however, given that the preference is less than 54%, this scarcely seems to be biologically significant (Fig. 2: mean \pm SEM of $53.61 \pm 0.94\%$ for correct token; $T=28$, $n=7$, $P=0.016$).

Upon further analysis, we found that overall, chimpanzees were more likely to return the higher-value token than the lower-value token (mean \pm SEM of $86.67 \pm 5.12\%$ for high-value token; $T=36$, $n=8$, $P=0.008$). The chimpanzees always showed a high probability of returning the higher-value red-striped token than the lower-value black token, regardless of which reward was offered, but interestingly they were more likely to return the higher-value token when the higher-value reward (grape) was offered than when the lower-value reward (squash) was offered (mean \pm SEM of $90.56 \pm 5.23\%$ for returning the high-value token when the higher-value reward was offered; mean \pm SEM of $82.78 \pm 5.15\%$ for returning the low-value token when the lower-value reward was offered; Wilcoxon Signed-Rank Test, $T=36.0$, $n=8$, $P=0.0078$). Apparently the chimpanzees not only show a preference for the higher-value token, but may be distinguishing between the higher-value and lower-value reward offerings as well.

Limited barter situation

This test also measured which of the tokens the chimpanzees preferred to return for each proffered reward, except in this situation, the tokens were limited and thus the chimpanzees could run out of the necessary tokens prior to the end of the session. For this test, the subject

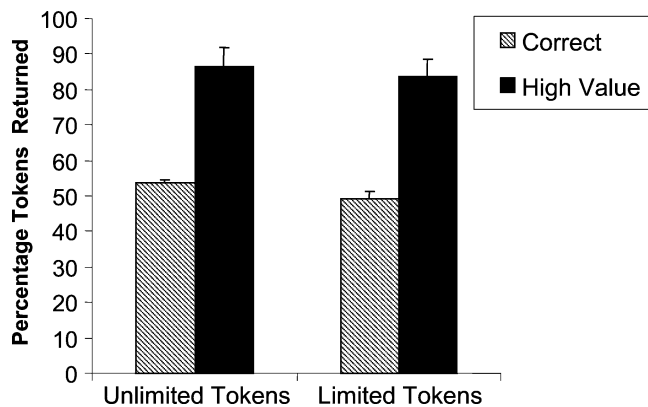


Fig. 2 The chimpanzees failed to return the “correct” token, that is the one that matched the proffered reward, in both the unlimited token test, in which they had guaranteed access to one of each token prior to each exchange, and the limited token test, in which tokens were not replaced during the session, thus planning had to be used to maximize rewards. However, in both situations, chimpanzees prefer the higher-value token (worth the higher-value food) over the lower-value token, returning higher-value tokens more frequently in the unlimited token test and prior to the lower-value tokens in the limited token test. This indicates that chimpanzees are following the simpler matching strategy (see Introduction) for resource acquisition, which requires only a single value association

was given three of each token prior to the commencement of the trial, and these tokens were not replenished during the trial. As a result, there was no guarantee how many of either token the subject would have access to for each exchange, and in fact, subjects could run out of one of the tokens before the end of the trial. Thus the chance probability of returning any one token was different for each exchange, dependent upon previous returns. Below we discuss expected returns for several different scenarios; please see Appendix for a mathematical calculation.

The number of correct returns was calculated per subject in the same manner as for the unlimited situation, which gave us a measure of whether or not subjects were returning the correct token overall. We looked at the percentage of correct returns and found that subjects did not return the correct token more frequently than the incorrect one (mean \pm SEM of $49.33 \pm 1.96\%$ for correct token; $T=12$, $n=6$, $P=0.844$).

We were unable to calculate token preference as we did for the unlimited situation, since each subject started out with three of each token and tokens were not replenished. Thus the null hypothesis (that is, the chance frequency of returning the tokens) changed with every exchange. To determine whether or not the subjects showed a preference for the higher-value token, we calculated which tokens they chose to return in the first half of each trial (that is, the first three of six total exchanges) as a proxy for the preferred token, assuming that they would choose to return first those tokens which they preferred. In other words, our null hypothesis was that we would expect, on average, 1.5 of each token returned in the first three exchanges (chance levels), so a preference would appear as an average of greater than 1.5 returns for one of the tokens in the first three exchanges (up to all three exchanges, which would indicate 100% preference). Overall, subjects showed a preference for returning first the higher-value token, the red striped token (mean \pm SEM of 2.51 ± 0.0799 higher-value tokens returned in the first three exchanges; $T=45$, $n=9$, $P=0.004$).

Cebus/Pan variation in the barter task

There was a difference in protocol between the capuchin monkeys and the chimpanzees such that the capuchin monkeys received somewhat less conditioning than chimpanzees (capuchins = 50 conditioning exchanges with each token, chimpanzees = 84 conditioning exchanges with each token), but other aspects, including prior experience and the human experimenter, were identical. Due to the pronounced sex difference in the way male and female capuchins responded to this test (Brosnan and de Waal 2004), we separated male and female capuchins for the purposes of the species comparison. Since there was only one male chimpanzee, we were unable to separate the chimpanzees by gender. As a result, the following analysis compares three groups

(chimpanzees, capuchin males, and capuchin females) rather than either two or four.

The three groups (chimpanzees, capuchin males, and capuchin females) showed no difference in the strength of preference for the high-value food reward (Fig. 3: mean \pm SEM of 96.67 ± 1.67 for chimpanzees; mean \pm SEM of 98.00 ± 2.00 for capuchin females; mean \pm SEM of 96.00 ± 4.00 for capuchin males; $F_{2,16} = 0.140$, $P = 0.870$) or the high-value token (mean \pm SEM of 71.91 ± 5.70 for chimpanzees; mean \pm SEM of 86.40 ± 4.62 for capuchin females; mean \pm SEM of 70.40 ± 7.49 for capuchin males; $F_{2,16} = 1.729$, $P = 0.209$). All three groups also showed a similar likelihood of returning the correct token in both the unlimited and the limited tests, in every case failing to return the token that matched the proffered reward (unlimited test: mean \pm SEM of 53.61 ± 0.94 for chimpanzees; mean \pm SEM of 50.94 ± 1.09 for capuchin females; mean \pm SEM of 53.81 ± 1.68 for capuchin males; $F_{2,16} = 1.546$, $P = 0.243$; limited test: mean \pm SEM of 49.33 ± 1.96 for chimpanzees; mean \pm SEM of 48.08 ± 4.18 for capuchin females; mean \pm SEM of 53.00 ± 4.37 for capuchin males; $F_{2,16} = 0.536$, $P = 0.595$).

The three groups did vary in their likelihood of returning the higher-value token in both the unlimited and the limited tests. The capuchin males were significantly less likely than the capuchin females or the chimpanzees to show a preference for returning the high-value token in the unlimited situation (mean \pm SEM of 86.67 ± 5.12 for chimpanzees; mean \pm SEM of 79.94 ± 7.14 for capuchin females; mean \pm SEM of 44.90 ± 4.54 for capuchin males; $F_{2,16} = 14.112$, $P < 0.001$). Furthermore, we compared the likelihood of returning the high-value token when the reward offered was the high-value reward versus the low-value reward and found that there was no interaction between reward

offered and group ($F_{2,32} = 0.748$, $p = 0.481$) nor was there an overall effect of which reward was offered on whether or not the higher-value token was returned ($F_{1,2,2} = 7.433$, $P = 0.103$), but there was an effect of group such that capuchin males were always less likely to return the higher-value token, regardless of the reward offered ($F_{2,2} = 36.244$, $P = 0.027$), which mirrors the previous results.

Finally, for the limited situation we used the percentage of high-value returns in the first half of exchanges per trial instead of the absolute number, as the chimpanzees had six exchanges per trial and the capuchins had ten exchanges per trial. The null hypothesis is that they would return both tokens, on average 50% of the time in the first half of exchanges. Chimpanzees were the most likely to return higher-value tokens, and capuchin males were significantly less likely to return more higher-value tokens in the first half of the trial in the limited token situation (mean \pm SEM of $83.70 \pm 4.91\%$ for chimpanzees; mean \pm SEM of $69.40 \pm 5.10\%$ for capuchin females; mean \pm SEM of $53.60 \pm 5.31\%$ for capuchin males; $F_{2,16} = 8.412$, $P = 0.003$). Taken together, these results indicate that capuchins and chimpanzees are remarkably similar in their response to the tests. All differences are apparently due to the response of male capuchins, rather than a species-specific difference.

Sex difference

Earlier we reported a sex difference for capuchin monkeys (Brosnan and de Waal 2004). Unfortunately we were unable to replicate this analysis for chimpanzees because we had only one male subject (at the time of testing he was the beta male of the group). However, it is of note that this male responded similarly to the females. In the unlimited test, he returned the 'correct' token 50.0% of the time (female average 54.06%) and returned the high value token 92.5% of the time (female average 85.94%). In the limited test he returned the 'correct' token 54.0% of the time (female average 48.75%). The only difference was that in the limited token test he returned the high value token only 58.33% of the time while the females returned the high value token 86.88% of the time.

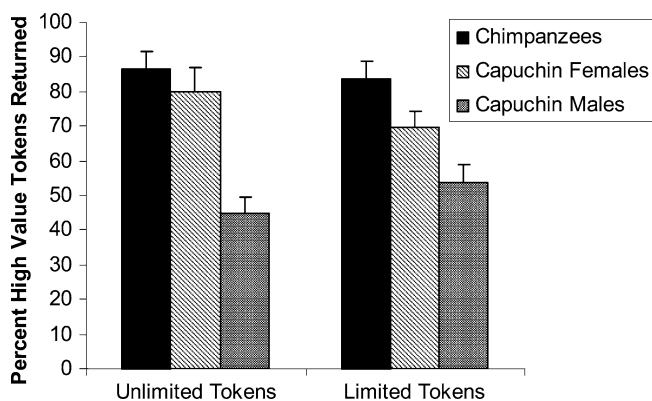


Fig. 3 Chimpanzees and capuchin females showed similar strategies for bartering both barter tasks, although capuchin males returned tokens at random. This indicates that, for this simple barter task, capuchin monkeys and chimpanzees show a similar strategy that may be the result of shared evolutionary heritage. These results support previous assertions that monkeys and apes, or in particular, *capuchins and chimpanzees*, show quantitative but not qualitative differences in cognition

Discussion

In our study, chimpanzees easily learned to associate value with different tokens. This is not surprising given that previously chimpanzees have been shown to respond to tokens (which represent foods) as the reward in a cognitive task (Sousa and Matsuzawa 2001). Furthermore, the chimpanzees' preference for the token was less strong than their preference for the food reward itself, which is expected given that the token has associated value while the reward has intrinsic value.

Finally, chimpanzees followed a consistent strategy of returning high-value tokens to barter for rewards.

These barter tasks were used to distinguish between the two different strategies of resource acquisition, the high value strategy and the matching strategy (see Introduction). The matching strategy, we argue, although ideal for obtaining more reward, requires more knowledge and planning than the high value strategy, as in the matching strategy, subjects must remember not only both token-reward associations (red striped token = grape, black token = squash), but must also pay attention to which reward is being offered to be successful. The high value strategy, on the other hand, requires only a single value association (high-value, red striped token > low-value, black token), and the subject need not pay attention to which reward is being offered, since the higher-value token is always returned. We used two different situations, one in which token access was unlimited and one in which token access was limited, to distinguish between these strategies.

Chimpanzees failed to return the correct token, both when their access to tokens was unlimited and limited. So, chimpanzee exchange behavior does not support the matching strategy, in which subjects maximize the overall number of rewards received. If our assumptions of what they must know are correct, evidently the chimpanzees 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 chimpanzees cannot do this conditional association task. There are several possibilities for why this may be. First, even in the limited task the chimpanzees 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 chimpanzees 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. Third, chimpanzees may not be used to an environment in which the commodities exchanged are truly limited. Many of the services they typically share, such as grooming, mating opportunities, or agonistic support are theoretically unlimited, as is food for this captive group, and so they may not be accustomed to the idea that some commodity can “run out”.

A final possibility is that this barter, in its similarity to a matching-to-sample stimulus equivalence test, is one that the chimpanzees cannot easily solve. Previous research indicates that chimpanzees (as well as all non-human species) have difficulty with the emergence of symmetry (Dube and McIlvane 1993), even if they are language competent (Dugdale and Lowe 2000) or have experienced training procedures designed to increase response (Yamamoto and Asano 1995). Our test differed

from other studies of symmetry equivalence in that we used two physical objects rather than lexigrams or matching-to-sample, but it is possible that the chimpanzees were unable to extrapolate symmetry in this case, either. However, it is interesting to note that the chimpanzee's response was not random, but showed a consistent preference for one token, indicating that they were at least paying attention to the task. This inability to extrapolate symmetry has interesting implications for reciprocity and exchange, since exchange requires correlating the symmetry between two different objects or services that are being traded. Perhaps this is one reason that nonhuman exchange behavior has never reached the level of complexity seen in humans.

However, the data do support the high value strategy. Chimpanzees preferred to return the higher-value token, the red token, regardless of which reward was offered. If our assumptions about what they must know or understand to follow the high value strategy are correct, these apes are using the simpler of the two possible mechanisms. In other words, they probably do not consider the explicit worth of each token. Instead, they may only recognize that the red token is the more highly valued of the two tokens, and hence show a strong preference for this token over the other.

There are several alternative explanations for this behavior that we cannot completely rule out. First, it may be that the chimpanzees are confusing this task with the earlier token preference tests, and hence are simply demonstrating their preference for the higher-value token. However, the chimpanzees have been subjected to food preference tests for years with no confusion. Furthermore, the token preference tests and the value association tasks were separated in time by a minimum of several days, and the tasks were set up in a different fashion, rendering it unlikely that such confusion was an issue. Another possibility is that the chimpanzees 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.

Earlier we asserted that chimpanzees, a species that participates frequently in interactions involving the exchange of multiple goods or services of varied value (de Waal 1997a), needs at least some ability to judge the value of different commodities in order to most effectively participate in such an exchange situation. Whether or not the high value strategy is sufficient is debatable. Clearly a situation in which the chimpanzees followed the matching strategy, returning the reward that matched the proffered token, would have strongly suggested such an ability. However, the chimpanzees have shown an ability to judge relative value, and have demonstrated preferences in a barter situation. It is possible that these skills, in typical chimpanzee interactions, would allow

them to gauge in a relative way what they should donate or accept, and thus participate in group exchange without significant cost. This may be particularly true if all individuals in the group are using relative rather than absolute judgments or if few commodities have explicit value.

Cebus/Pan comparison

Overall, the chimpanzees performed very similarly to the capuchin monkeys. While it is true that the capuchin males showed divergence from the chimpanzees and capuchin females, the fact that females do show this behavior indicates that the species is capable of barter (Brosnan and de Waal 2004). Both capuchins and chimpanzees easily learned to prefer one token to the other, and both showed a stronger preference for the food rewards than for their associated tokens. Moreover, in the barter task, both species reacted similarly and demonstrated the cognitively simpler of the two proposed strategies. This similarity is a bit unexpected given the general finding that chimpanzees outperform capuchins on cognitive tasks, even if there is debate over whether the differences between the species are quantitative or qualitative (Anderson 1996; Tomasello and Call 1994, 1997; Visalberghi 1997).

Chimpanzees show a stronger ability than capuchins to imitate arbitrary actions (Custance et al. 1995) or “food” processing strategies (artificial fruit task: Custance et al. 1999; Whiten et al. 1996), and to complete tool use tasks (trap-tube task: Limongelli et al. 1995; Visalberghi and Limongelli 1996). However, such differences need to be treated with caution, because even though one research team has found chimpanzees to be more coordinated on a cooperative task than capuchins (Chalmeau, 1994; Chalmeau and Gallo 1996; Chalmeau et al. 1997), another team reports significant capuchin coordination (Mendres and de Waal 2000). Finally, in a computerized chase task in which the subjects controlled a cursor, which competed with a computer-controlled cursor to contact a moving target first, capuchins and chimpanzees ranked equivalently when the cursors were visually distinct and the computer-controlled cursor moved randomly (Jorgensen et al. 1995). However, when the cursors were visually identical and the computer-controlled cursor followed an algorithm to “chase” the target, clearly a more complex task, chimpanzees significantly outperformed capuchins.

It appears that chimpanzees and capuchins may show similar cognitive abilities on simple tasks, but not on more complex ones. Based on previous findings, we had predicted that the chimpanzees might show the cognitively more complex matching strategy, and it is somewhat surprising that they, like the capuchins, follow the high value strategy. Perhaps chimpanzees have not have developed the cognitive machinery to deal with such a situation.

Apparently in the domain of barter, chimpanzees and capuchin monkeys show convergence in their cognitive approach. As social exchange is a big part of both of these species’ social organization, perhaps it was equally important for both species to develop an ability to monitor exchange, thus leading to similar responses in this task, while in other arenas their cognitive capacities diverged. Further comparative studies will allow us to clearly delineate those areas in which these often-compared primates show similarities and differences, which will allow us a greater understanding of the effect of social environment on cognitive evolution.

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Appendix 1: Calculations for determining expected frequency of reward returns

There are twenty ways to randomly arrange three high-value rewards and three low-value rewards in a series of six trials. These can be divided into four basic classes.

- Three high-value rewards followed by three low-value rewards (one possibility)
- Two high-value rewards and one low-value reward in the first three trials, followed by one high-value reward and two low value rewards in the second three trials (nine possibilities)
- One high-value reward and two low-value rewards in the first three trials, followed by two high-value rewards and one low-value reward in the second three trials (nine possibilities)
- Three low-value rewards followed by three high-value rewards (one possibility)

If the arrangements of the trials is truly random, each possibility is equally likely, making it nine times more likely that a series will fall into the second or third class than into the first or fourth. By calculating the return generated by a particular strategy in each class of trial, multiplying those returns by the probability of encountering each class, and adding the products, we can calculate the expected return of that strategy under these conditions.

An individual pursuing the matching strategy will receive three high-value rewards and three low-value rewards from any of these trials, yielding an expected return of three high-value rewards and three low value rewards.

$$E(\text{reward}) = \frac{1}{20}(3H + 3L) + \frac{9}{20}(3H + 3L) \\ + \frac{9}{20}(3H + 3L) \frac{1}{20}(3H + 3L) \\ E(\text{reward}) = 3H + 3L$$

An individual pursuing the high value strategy with limited tokens will return the high-value tokens followed by the low-value tokens, with a total return ranging from three high-value rewards and three low-value rewards to no reward at all. The expected return is 1.5 high-value rewards and 1.5 low-value rewards.

$$E(\text{reward}) = \frac{1}{20}(3H + 3L) + \frac{9}{20}(2H + 2L) \\ + \frac{9}{20}(1H + 1L) \frac{1}{20}(0H + 0L) \\ E(\text{reward}) = \frac{1}{20}(3H + 3L + 18H + 18L + 9H + 9L) \\ = \frac{1}{20}(30H + 30L) \\ E(\text{reward}) = \frac{3}{2}H + \frac{3}{2}L$$

An individual pursuing the high value strategy with unlimited tokens will return high-value tokens for every trial. The expected return is three high-value rewards.

$$E(\text{reward}) = \frac{1}{20}(3H + 0L) + \frac{9}{20}(3H + 0L) \\ + \frac{9}{20}(3H + 0L) \frac{1}{20}(3H + 0L) \\ E(\text{reward}) = \frac{1}{20}(3H + 27H + 27H + 3H) = \frac{60}{20}H \\ E(\text{reward}) = 3H$$

An individual pursuing random strategy will return tokens with no regard to their value. For any given series of trials with limited tokens, there is a 1/20 chance that the individual will match the trials perfectly, a 9/20 chance that the individual will miss one low-value and one high-value reward, a 9/20 chance that the individual will miss two low-value and two high-value rewards, and a 1/20 chance that the individual will not match any trials correctly. The results are restricted to these four combinations (3 and 3, 2 and 2, 1 and 1, 0 and 0) because of the token-limited nature of the trials. The expected return is 1.5 high-value rewards and 1.5 low value rewards, using calculations similar to those in the token-limited maximum value strategy.

An individual pursuing the random strategy in a series of trials with freely available tokens has a 1/2 chance of earning a reward on each trial. This arrangement provides a much wider spectrum of possible reward combinations than does the token-limited situation, as the numbers of high-value and low-value rewards are no longer constrained to be equal, but the expected return does not change.

$$E(\text{reward}) = 3 \times \frac{1}{2}H + 3 \times \frac{1}{2}L \\ E(\text{reward}) = \frac{3}{2}H + \frac{3}{2}L$$

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