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# Food-exchange with humans in brown capuchin monkeys

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**Abstract** To assess how brown capuchin monkeys (*Cebus apella*) delay gratification and maximize payoff, we carried out four experiments in which six subjects could exchange food pieces with a human experimenter. The pieces differed either in quality or quantity. In qualitative exchanges, all subjects gave a piece of food to receive another of higher value. When the difference of value between the rewards to be returned and those expected was higher, subjects performed better. Only two subjects refrained from nibbling the piece of food before returning it. All subjects performed two or three qualitative exchanges in succession to obtain a given reward. In quantitative exchanges, three subjects returned a food item to obtain a bigger one, but two of them nibbled the item before returning it. Individual differences were marked. Subjects had some difficulties when the food to be returned was similar or equal in quality to that expected.

**Keywords** Reciprocity · Gift · Value · Economics · Self-control · *Cebus apella*

## Introduction

Exchanges and gifts are a main tenet of modern human economies and traditional cultures (Mauss 1924; Sahlins 1972). The exchange of commodities also underlies many instances of cooperation among animals. It requires individuals to make choices based on the value of the commodities offered (Noë et al. 2001). Unlike cases involving human beings, however, most exchanges among animals rely on mechanisms that do not involve cognitive processes. Selective pressures may promote reciprocity by shaping specific signals or threshold responses. The ability to compare values of commodities and to delay behavioral responses would lead to improved performances, however, which would favor the selection of such cognitive abilities. As stressed by Marshall (1920), value always means exchange value. Correlations between given and received actions have been cited as evidence for reciprocity in social grooming, food sharing, and agonistic support (Seyfarth 1980; de Waal and Luttrell 1988; de Waal 1989; Manson et al. 1999). However, it is difficult to demonstrate that individuals calculate reciprocity and interchange in the social context (Seyfarth and Cheney 1988; Hemelrijk 1996; de Waal 1997a). For a behavioral tactic to be "economical," it has to yield a maximum payoff (Noë et al. 2001).

Active giving of food is not common among non-human primates (Feistner and McGrew 1989; Thierry et al. 1989). It regularly occurs only in marmosets and tamarins, who may offer food to infants using particular vocalizations and postures. It is more rarely reported in pongids. Most food transfers observed in non-human primates result from tolerated scrounging, which means that the possessor allows a group-mate to remove food being held or eaten (Feistner and McGrew 1989; Thierry et al. 1989; de Waal 1989). Such passive food sharing has been described in capuchin monkeys both in the wild and in captivity (*Cebus* sp.: Thierry et al. 1989; de Waal et al. 1993; Perry and Rose 1994; Fragaszy et al. 1997). In brown capuchins (*C. apella*), a relatively high level of tolerance allows individuals to sometimes take food from a dominant possessor's hands or mouth. Transfers of food and objects among group members vary with physical parameters. They are more likely to occur with valuable items that are easy to carry and escape with (Thierry et al. 1989). The relevance of object portability was also shown in long-tailed macaques (*Macaca fascicularis*: Kummer and Cords 1991).

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In experiments where brown capuchins are separated by a wire-mesh partition, food transfers occur but they are mainly passive. An individual collects pieces of food that another has dropped near the mesh (Westergaard and Suomi 1997; de Waal 1997b, 2000). Such facilitated taking occurs mainly between females linked by affiliative relationships. It is also more common for less favored foods (de Waal 1997b, 2000). Moreover, when two capuchins have to work jointly to obtain rewards, they tolerate taking from the partner more readily than if they obtain the rewards individually. Such behavior may result from attitudinal reciprocity based on mutual tolerance rather than calculated reciprocity based on cognitive processes (de Waal 2000; de Waal and Berger 2000). With chimpanzees (*Pan troglodytes*) tutored in a symbol language, an individual would request a tool from another and give it food in exchange (Savage-Rumbaugh et al. 1978).

Chimpanzees can postpone immediate rewards for future, more attractive rewards (Beran et al. 1999), and they are skillful in quantity judgments (Boysen 1997; Tomasello and Call 1997). Lefebvre (1982) studied a young chimpanzee who engaged in reciprocal exchanges with a human experimenter. The subject's behavior depended on the respective values of the food offered in the exchange. When a preferred food was requested by the experimenter, the chimpanzee quickly learned to give back the smallest permissible amount of food, thus maximizing its gains. More generally, chimpanzees may barter without training (Lefebvre and Hewitt 1986; Hyatt and Hopkins 1998) and they may even stock tokens used to get rewards (Sousa and Matsuzawa 2001). Another study showed that gorillas (*Gorilla gorilla*) would return several objects in succession before obtaining a reward from an experimenter (Chalmeau and Peignot 1998). In monkeys, spontaneous giving toward human beings has been reported in a macaque (*Macaca nemestrina*: Bertrand 1976) and a mangabey (*Cercocebus torquatus*: Coussi-Korbel 1993). In both cases, the subject gave something of little value to itself to obtain a more prized food, but no comprehensive testing was carried out. A brown capuchin monkey used chips as tokens to request food (Westergaard et al. 1997). Moreover, brown capuchins recognize exchange opportunities; that is, they give food to an experimenter to receive a qualitatively more desirable reward (Westergaard et al. 2004) and they may also reject an exchange if they witness a conspecific obtain a more desirable reward (Brosnan and de Waal 2003).

It appears that brown capuchin monkeys will trade low-valued objects for higher-valued objects. We assessed the ability of brown capuchin monkeys to delay gratification and trade not only on a qualitative basis, but also when food rewards differed in quantity. In four experiments, the subjects could give back a reward to a human experimenter to receive another reward differing in quality or quantity.

## Methods

### Subjects and conditions

We tested six brown capuchin monkeys: one female (Aso, 13 years old) and five males (Clo, 11; Bib, 7; Acc, 5; Arn, 4; and Pis, 3 years). They belonged to a social group of 16–18 individuals, kept at the Primate Center of the Louis Pasteur University, Strasbourg. The animals were housed in an enclosure composed of two indoor compartments (33 $m^2$ total) and four outdoor wire-mesh compartments (45 $m^2$ total). Commercial monkey diet and water were available ad libitum in the indoor rooms. Subjects were never deprived of food. The enclosure was furnished with wooden perches and suspended plastic barrels. The ground of the outdoor enclosure was covered with sand and gravel. Compartments were connected by sliding doors. For testing, subjects were individually separated from the rest of the group in an outdoor compartment.

### Assessment of food preferences

Prior to the four experiments, we assessed the subjects' preferences for four different types of food: monkey diet pellets, cookies, carrots, and apples. The food was cut into small pieces approximately $2 \times 1 \times 0.5$ cm. In each trial, the experimenter sat in front of the wire mesh and presented two food items to the subject, one in each hand. The experimenter randomly changed hands across presentations. A second experimenter recorded which item the subject took. Trials were separated by 30-s intervals. Six sessions of 15 trials were carried out for each subject, including all combinations of two different food items, presented in random order. For each subject, sessions were separated by at least 30 min. The preference order was: cookie > apple > carrot > pellet (Table 1).

We also verified that subjects preferred a bigger piece of cookie to a smaller one. In each trial, the experimenter presented two pieces of cookie to the subject, one in each hand. One piece was $2 \times 1 \times 0.5$ cm and the other $1 \times 1 \times 0.5$ cm. One session of 15 trials was carried out for each subject. All subjects took the bigger piece of cookie in 12 or 13 trials out of the 15.

### Pre-experimental period

The experimenters shaped the exchange action by the monkeys in several steps. The first subject, Bib, was observed repeatedly throwing a handful of sand and pebbles through the fence when humans were near the enclosure. The experimenter encouraged this behavior by giving items (e.g., raisins) to Bib each time he threw something. Subsequently, the subject was rewarded only when it threw a single object or pebble picked from the

**Table 1** Subjects' food preferences and exchanges for combinations of two food items. For food preferences, two items were presented simultaneously to the subject (*column 1* and *columns 2–5*). For food exchanges, the subject had to give back the first item received (*column 1*) to obtain the second one (*columns 6–9*)

| Subject | Food preferences | | | | Food exchanges | | | |
|---|---|---|---|---|---|---|---|---|
| | Items chosen by the subject (%) | | | | Items given back by the subject (%) | | | |
| | Pellet | Carrot | Apple | Cookie | Pellet | Carrot | Apple | Cookie |
| Clo | | | | | | | | |
| Pellet | – | 67 | 100 | 100 | – | 100 | 100 | 100 |
| Carrot | 33 | – | 93 | 73 | 100 | – | 100 | 100 |
| Apple | 0 | 7 | – | 93 | 7 | 20 | – | 73 |
| Cookie | 0 | 27 | 7 | – | 0 | 0 | 0 | – |
| Aso | | | | | | | | |
| Pellet | – | 86 | 100 | 100 | – | 100 | 100 | 100 |
| Carrot | 14 | – | 100 | 100 | 93 | – | 100 | 93 |
| Apple | 0 | 0 | – | 100 | 13 | 27 | – | 47 |
| Cookie | 0 | 0 | 0 | – | 20 | 7 | 13 | – |
| Acc | | | | | | | | |
| Pellet | – | 67 | 67 | 100 | – | 93 | 100 | 100 |
| Carrot | 33 | – | 100 | 100 | 80 | – | 100 | 100 |
| Apple | 33 | 0 | – | 93 | 7 | 7 | – | 40 |
| Cookie | 0 | 0 | 7 | – | 0 | 0 | 0 | – |
| Bib | | | | | | | | |
| Pellet | – | 53 | 100 | 100 | – | 67 | 100 | 100 |
| Carrot | 47 | – | 100 | 100 | 47 | – | 100 | 100 |
| Apple | 0 | 0 | – | 80 | 0 | 0 | – | 13 |
| Cookie | 0 | 0 | 20 | – | 0 | 0 | 0 | – |
| Arn | | | | | | | | |
| Pellet | – | 100 | 100 | 100 | – | 93 | 93 | 100 |
| Carrot | 0 | – | 100 | 100 | 20 | – | 87 | 100 |
| Apple | 0 | 0 | – | 93 | 7 | 0 | – | 60 |
| Cookie | 0 | 0 | 7 | – | 0 | 0 | 0 | – |
| Pis | | | | | | | | |
| Pellet | – | 87 | 93 | 93 | – | 93 | 100 | 100 |
| Carrot | 13 | – | 67 | 80 | 93 | – | 100 | 100 |
| Apple | 7 | 33 | – | 93 | 0 | 0 | – | 7 |
| Cookie | 7 | 20 | 7 | – | 0 | 0 | 0 | – |

ground of the enclosure. In a third step, the subject was rewarded only when it threw the object toward the hand of the experimenter. In a fourth step, the subject was required to put the object in the hand of the experimenter. At each step, there were between 10 and 20 occurrences of object throwing or giving per week rewarded by the experimenter. Training Bib took 2 months. Experiments 1–4 reported below were then carried out on this subject.

After completion of the first set of experiments, Bib was regularly rewarded when he gave objects to people. Three months later, a second subject, Acc, started to throw objects through the fence. During a 2-month period, we repeated the same procedure used with Bib to train Acc in object exchange, but using between 20 and 30 trials per workday. Two other subjects, Clo and Aso, started to throw objects, respectively, 6 and 9 weeks after Acc's training started. We applied the same training procedure to both subjects and within 1 month they reliably exchanged objects with humans. These four monkeys were regularly rewarded for giving objects to people. One year later, two further monkeys, Arn and Pis, started to throw objects. Following similar training, they exchanged objects with humans within 2 weeks. Acc, Clo, Aso, Arn, and Pis were each run in experiments 1–4.

## Testing procedure

We separated the subject from the others in an outdoor compartment for testing. The experimenter stood in front of the wire mesh with one food item in each hand and showed them to the subject for 2 s (Fig. 1a). Then he gave one item to the subject (Fig. 1b). The experimenter withdrew both hands for 5 s, then held out the empty hand while showing the second item on the other hand. If the subject gave back the first item (or part of it) by putting it in the experimenter's hand (Fig. 1c), it was allowed to take the second item (Fig. 1d). If the subject did not give back the first item, the experimenter gave nothing and the trial ended. The experimenter randomly changed hands to present the items. The experimenter recorded the subject's behaviors: exchange, no exchange, item returned intact, or item nibbled by the subject. In the latter case the fraction of the item returned was recorded. Trials were separated by 30 s and sessions by at least 30 min. Each subject was run in no more than two sessions per half-day.

## Preliminary testing

Prior to experiments 1–4, we verified that subjects would give back either a non-edible object (a small stone) or a


**Fig. 1** Exchange sequence. **a** The experimenter presents a piece of cookie in the left hand and a piece of carrot in the right hand. **b** The experimenter gives the carrot to the subject. **c** The subject puts the carrot back in the hand of the experimenter. **d** The subject is allowed to take the cookie

food item (a pellet) to obtain a piece of apple. We carried out two sessions of 15 trials for each type of exchange. For stone versus apple, five subjects gave the stone back to the experimenter from the very first trial, at 100% success in both sessions. The sixth subject (Aso) succeeded from the fourth trial, at 100% success afterward. For pellet versus apple, all subjects exchanged the pellet for the apple from the very first trial and scored 100% success in both sessions.

## Results

### Experiment 1: exchanging foods differing in quality

We tested whether the subjects would exchange food items that they valued differently in preference tests. We used the four kinds of items previously assessed on the food preference trials: pellet, carrot, apple, and cookie, in $2 \times 1 \times 0.5$ cm pieces. On each trial, the experimenter first offered one type of item, then proposed another type to the subject. There are 12 possible paired combinations of items. We conducted 15 sessions of 12 trials each, corresponding to the 12 combinations of items, presented in random order to every subject.

Because of the small sample size and the great variability of the subjects' performances, results were analyzed separately for each individual. The percentage of exchanges performed by each subject for all combinations of items is presented in Table 1. The subjects regularly exchanged the less valued items (pellet and carrot) for one another. Exchanges between the more valued items (apple and cookie) were less frequent; a cookie was almost never returned whereas an apple could be exchanged for a cookie, depending on the subject (Table 1). The subjects consistently gave back one of the less valued items (pellet and carrot) to obtain one of the more valued items (apple and cookie); they rarely exchanged in the other direction (Table 1). The differential exchange scores for different combinations of items are consistent with the preferences of subjects as measured in the food preference trials (Table 1). The correlation between the matrix of preferences and the matrix of exchanges was calculated for each subject using Mentel's $Z$ statistic (Matman program, Noldus: de Vries et al. 1993). This yielded correlations that ranged from $+0.56$ to $+0.91$, although these did not reach statistical significance because of the small sample size.

The monkeys sometimes nibbled part of an item before returning it to the experimenter. This occurred in a minority of exchanges for four of the subjects: 1.7, 6.7, 5.0, and 5.6% of trials for Clo, Aso, Acc, and Arn, respectively. In contrast, the other two subjects, Pis and Bib, nibbled the item in 33.0 and 51.7% of the trials, respectively, before exchanging it.

Brown capuchin monkeys exchanged food with an experimenter to obtain the maximum payoff, consistent with previous results (Westergaard et al. 2004). The subjects gave a piece of food to receive one of a different kind but of higher value. In doing so, the subjects followed their food preferences. The wider the perceived difference between the value of the food, the more likely was the exchange. The subjects generally refused to give a prized food for a less valued one. There were some

exceptions to this rule, and subjects occasionally exchanged in the reverse direction, but similar behaviors were observed in the food preference tests. Two monkeys frequently nibbled the first item before returning it. By decreasing the quantity of the returned piece of food, they altered the exchange situation to maximize payoff.

## Experiment 2: returning a whole food item

In experiment 1, subjects were reluctant to exchange a piece of apple for a piece of cookie, even though the latter was preferred. The fact that the subjects were allowed to return an item after nibbling could have biased the rates of exchange. The second experiment assessed the influence of this factor.

We ran the subjects on 8 or 15 sessions of 12 trials in which they first received a piece of apple, which they had to return to receive a piece of cookie. For the first 8 sessions, the procedure was the same as previously described. From the 9th session, the subjects were given the second item (piece of cookie) only if they had returned the first item intact.

The results are shown in Fig. 2. Pis never exchanged, and Clo and Acc almost ceased to exchange from the 2nd trial. We stopped testing these subjects after the 8th session. Aso rapidly learned to return the whole piece of apple to receive the cookie (Fig. 2a). We also stopped testing her after the 8th session. Bib's exchange score progressively increased from the 1st to the 8th session (Fig. 2a) but he always nibbled the item before returning it. When the experimenter required that the item be returned intact, Bib's exchange behavior progressively disappeared. He did not learn to return an entire item (Fig. 2b) and we stopped testing him after the 15th session. Arn consistently exchanged during the first 8 sessions. On the 9th session, he did not return the full item, but he did so from the 10th session. He then typically returned the entire item until testing stopped after the 15th session (Fig. 2b).

Three subjects failed to exchange between two preferred foods right from the start, and a fourth failed to return an intact item. Two others succeeded in the task, one from the start, the other progressively across trials. These results show that a capuchin monkey may implement a strict exchange rule on a qualitative basis, but that the task is quite demanding. It is possible that the change of the rules between experiments 1 and 2 was confusing to some of the subjects, which would explain their low performance.

## Experiment 3: exchanging foods differing in quantity

In this experiment, we investigated the subjects' performance on quantitative exchanges, that is, their ability to return a small quantity of food for a larger quantity of the same food. Since experiment 2 showed that exchanges might extinguish when nibbling was forbidden, partial returns were accepted.

We ran 15 sessions of 12 trials in which the subjects were first given a piece of cookie. If they returned it to the experimenter they obtained a piece of cookie twice the size of the first one. The exchange procedure was the same as previously. The experimenter first gave the subject a $1 \times 1 \times 0.5$ cm (0.3 g) piece of cookie, exchangeable for a $2 \times 1 \times 0.5$ cm piece of cookie. The subject was allowed to consume part of the first item before returning it. The second experimenter scored the size of the returned item: whole, half, one-third, one-fourth, or one-eighth of the original.

Results are presented in Fig. 3. Clo, Aso, and Pis did not exchange (Fig. 3a). We stopped testing them after the 9th session. The other subjects gave back a small item to receive a bigger one in a majority of the trials beginning from the 2nd or the 3rd session. Their

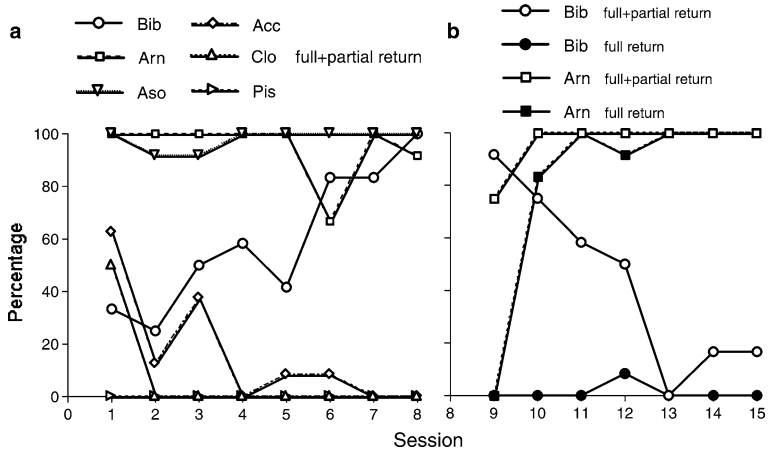


**Fig. 2** Exchanging apple for cookie (experiment 2). **a** Percentage of exchanges in which the apple item was fully or partially returned (six subjects). Pis, Clo, and Acc failed to give any of the apple back. Aso and Arn made regular exchanges. Bib consistently increased his exchange rate. **b** Percentage of exchanges when the experimenter required that the entire apple item be returned (two subjects). *Clear dots* item fully or partially returned. *Black dots* whole item returned. Bib failed to give back the whole apple item and he stopped gradually making exchanges. Arn learned to return the whole apple item

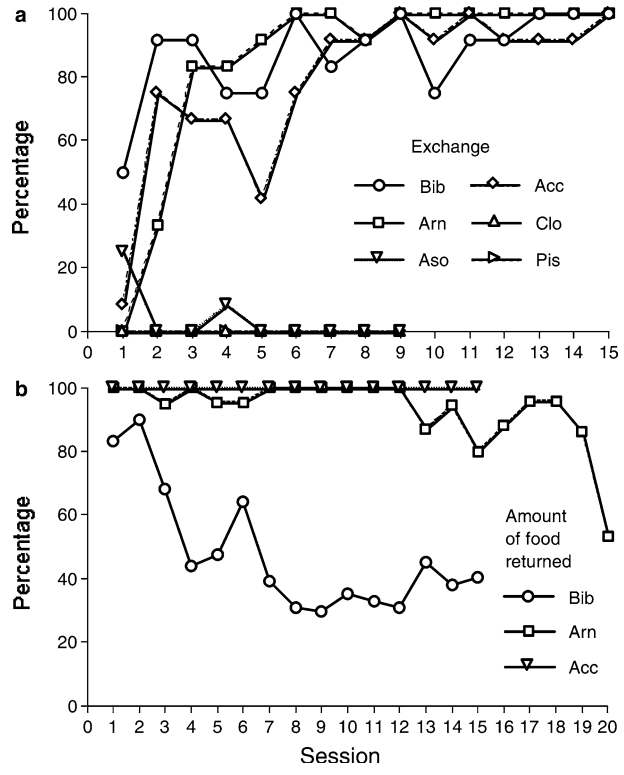


**Fig. 3** Quantitative exchanges (experiment 3). **a** Percentage of exchanges throughout sessions (six subjects). Aso, Pis, and Clo failed to exchange. Acc, Bib, and Arn gave back a small piece of cookie to obtain a bigger one. **b** Amount of food given back (three subjects): sum of the fractions of food items returned in exchanges. Acc always returned the whole item. Bib learned to decrease the quantity of food given back within the first 7 sessions. Arn needed 20 sessions to reach an equivalent stage

performances reached between 70 and 100% success from the 6th session (Fig. 3a). Acc returned the whole food item on most trials (Fig. 3b). Bib again always nibbled off part of the item before giving it back. Furthermore, as sessions progressed, Bib decreased the amount of cookie given back. He ate between 60 and 70% of the initial piece from the 9th to the 15th session (Fig. 3b). Arn exchanged a small item for a bigger one from the beginning. During the first 12 sessions he did not decrease the amount of food returned, but then he sometimes nibbled before giving it back. We ran Arn on 5 additional sessions and he returned increasingly smaller amounts of cookie (Fig. 3b).

In this experiment, when the monkeys had to inhibit the immediate consumption of one piece of food to get a bigger piece, only the female subject returned the whole piece of food. Two older males and a younger one did not return the original item to obtain a piece twice the size. The other two males nibbled the food before returning it, thus their behavior should not be described as genuine exchange. As the experimenter accepted nibbling, the monkeys did not inhibit this behavior. By the end of the experiment, they consistently gave back no more than one-third of the original piece received, thereby maximizing the payoff. Another explanation is that they simply returned the remaining piece of food; in many cases, however, they nibbled the food just before the experimenter requested exchange. Similar behavior was reported in exchanges between a young chimpanzee and an experimenter (Lefebvre 1982).

### Experiment 4: exchanging two or three items in succession

In experiments 1–3, we tested whether the subjects would exchange one item for another. In experiment 4, the final reward was delayed. We investigated whether subjects would perform double or triple exchanges, that is, if they would return two or three items successively to obtain another.

For double exchanges, we carried out two sessions of 12 trials each, using items of increasing attractiveness to the subjects. The experimenter showed a pellet (item 1) and a piece of apple (item 2) in one hand (out of the subject's reach) while presenting the palm of the other hand. The subject had to pick up a stone from the floor and put it in the experimenter's empty hand. Then, the experimenter offered the pellet with one hand while presenting the piece of apple in the other hand (out of the subject's reach). If the subject took the pellet, 5 s later the experimenter held out one empty hand while showing the piece of apple on the other hand. If the subject returned the pellet, it was allowed to take the piece of apple. We also ran triple exchange trials. The procedure was the same as before but we used stone, pellet, carrot, and apple as consecutive items.

In double exchanges, all subjects succeeded from the first trial and scored 100% success in all sessions. In triple exchanges, five subjects succeeded from the first trial and reached 100% success in all sessions; the sixth subject, Pis, succeeded in 75 and 67% of trials in the first and second sessions, respectively.

Being aware of the final reward, capuchins delayed gratification and returned two or three items in succession to obtain it. The task appeared easy, in view of the rapid success of all individuals. This contrasts with a similar study in gorillas in which a few individuals succeeded in double and triple exchanges (Chalmeau and Peignot 1998). Unlike the capuchins, the gorillas were not separated for testing, and the presence of conspecifics may have impaired their performances.

## Discussion

Brown capuchin monkeys maximized payoffs when requested to exchange on a qualitative basis (experiment 1). The performances of most subjects decreased when the experimenter required them not to nibble the original item before returning it (experiment 2), or to exchange on a quantitative basis (experiment 3). The significant variability in the subjects' performance is a main result of this study. Though the small sample size

did not allow assessment of the role of factors such as age or sex, these results indicate that full exchange is not a species universal, at least in our experimental conditions. Not only did the monkeys encounter difficulties with quantitative exchanges, they also behaved less effectively in qualitative exchanges when the difference in value between rewards was low. In another study, capuchin monkeys trained to associate tokens with low-value and high-value food rewards performed poorly when required to exchange them according to their value (Brosnan and de Waal 2004).

For an animal to exchange profitably, it should be endowed with at least two kinds of abilities. First, it should have the cognitive skill needed to compare the characteristics of two commodities and make use of "more" and "less" value judgments (Boysen 1997). The results of experiments 1–3 show that the brown capuchins can make such a judgment, consistent with what we know about their cognitive capacities. In general, they have good learning and memory abilities, are skillful in problem solving, and are good tool users (Visalberghi and Limongelli 1996; Anderson 1996, 2002; Tomasello and Call 1997). Second, the animal should display self-control; that is, individuals should be able to choose a more valued delayed reward over a less valued immediate reward (Logue 1988). Monkeys are able to delay gratification (Tobin et al. 1996; Anderson 2001; Szalda-Petree et al. 2004). In the present study, withholding consumption of one piece of food to get another is evidence of self-control. Interestingly, it was not rare to see a subject holding the first piece in its mouth before taking it out to exchange it. Experiment 4 also showed that brown capuchins could perform a sequence of two or three qualitative exchanges. It appears that the extent of self-control required by a quick sequence of qualitative exchanges is less than for quantitative exchanges.

By human standards, brown capuchins appear impulsive. When employing tools and trying to solve problems, they use mainly "non-anticipatory strategies," meaning that they attempt numerous combinations of objects and actions without real foresight (Visalberghi and Limongelli 1996). The enactment of complex goal-directed behaviors requires individuals to monitor the consequences of their behavior. This depends in particular on the ability to delay gratification, as has been proposed for human beings (Mischel 1974). Capuchins probably apply the same skills in the social realm (Brosnan and de Waal 2003). The present results confirm or extend the conclusions of previous studies. Brown capuchin monkeys possess the basic skills necessary to exchange, with the caveat that they often altered the nature of the exchange by returning only part of the initial food item. In addition, they found it difficult to exchange when the food to be returned was similar or equal in quality to the one still to be obtained. Further studies should examine whether this arises from limitations in assessing differences in quality and quantity, or from an inability to delay gratification when the subsequent reward value is relatively low.

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