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ORIGINAL PAPER

Monkeys fail to reciprocate in an exchange task

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Abstract Exchanges form the basis of human economies. Animals too can engage in reciprocal interactions but they do not barter goods like humans, which raises the question of the abilities necessary for trading to occur. Previous studies have shown that non-human primates can exchange food with human partners. Here, we tested the ability of brown capuchin monkeys and Tonkean macaques to reciprocate in a task requiring two conspecifics to exchange tokens in order to obtain rewards from an experimenter. We recorded 56 transfers between subjects in capuchin monkeys and 10 in Tonkean macaques. All transfers were passive in both species. Capuchins preferentially picked up tokens valuable for them in the partner's compartment. They tended to manipulate the partner-valued tokens more often than the no-value ones, leading to more opportunities for these tokens to end up within reach of the partner. Despite optimal conditions where values of goods were defined and known by partners, however, none of the pairs tested engaged in short-term reciprocal interactions. These results indicate that calculated reciprocity was difficult if not impossible in the animals tested.

Keywords Reciprocity · Token · Trading · Economics · Primates

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Introduction

Gift and exchange lie at the core of human societies (Mauss 1923/1924); they form the basis of their economies. In traditional societies, individuals provide goods for the community; they share the benefits of their skills with others, thus sustaining what has been called natural economics (Sahlins 1972). In Western societies, economics mainly relies on expected reciprocity; goods are traded for others, which give rise to formalist economics. Exchanges of goods or favors are reported in nature too (Dugatkin 1997). The theory of biological markets even proposes that cooperation between animals obeys to the law of supply and demand, but it does not assume that individuals calculate reciprocity (Noë and Hammerstein 1994). Actually, animals do not reciprocate at the rates observed in humans, based on expected returns, which raises the question of the skills necessary for trading to occur.

Different categories of reciprocation have been reported among unrelated individuals in non-human primates. Partners linked by social bonds interact in a symmetrical way when they react similarly to each other without stipulating equivalent returns ('symmetry-based reciprocity': de Waal and Luttrell 1988). Alternatively, when partners behave positively toward each other as a consequence of

prior friendly interactions, both mirror the partner attitude, leading to either short-term ('attitudinal reciprocity': de Waal 2000) or long-term reciprocal interactions ('emotional bookkeeping': Aureli and Schaffner 2002).

A further mode of reciprocation is based on the mental scorekeeping of given and received favors, similar to the calculations involved in the trading of human economics. Such calculated reciprocity could account for the exchange of services like grooming and support in conflict, for instance (Seyfarth and Cheney 1984; de Waal and Luttrell 1988). Correlations drawn from observations in the social context are yet insufficient to demonstrate contingencies between gifts and receipts (Hemelrijk 1996). To assess whether exchanges are based on calculated reciprocity, one need to show experimentally that goods are transferred in both directions between partners and that gifts are conditioned by receipts. In experiments based on the exchange of tokens between conspecifics, great apes showed difficulties in transferring tokens to their conspecific partners (chimpanzees: Brosnan and Beran 2009; chimpanzees, bonobos, gorillas: Pelé et al. 2009). However, we recently showed that a pair of orangutans (*Pongo pygmaeus*) could achieve reciprocal and balanced transfers based on expected returns (Dufour et al. 2009).

In monkeys, macaques and capuchins possess some of the cognitive prerequisites required for calculated reciprocity. They form long-lasting bonds, they can delay gratification (Ramseyer et al. 2006; Amici et al. 2008; Pelé et al. 2010a, b) and estimate the quantity and quality of goods (Addessi et al. 2007, 2008a, b; Beran 2008; Beran et al. 2008; Cantlon and Brannon 2006; Drapier et al. 2005; Evans et al. 2009; Padoa-Schioppa et al. 2006; van Marle et al. 2006). In experimental situations, macaques and capuchins also show the capacity to exchange non-edible items (Westergaard et al. 1998, 2004; Brosnan and de Waal 2004a, b; de Waal et al. 2008) and edible items (Drapier et al. 2005; Ramseyer et al. 2006; Pelé et al. 2010a, b) with humans. When considering exchanges between conspecifics, individuals of two groups of captive capuchins have been observed transferring tools and food from one group to the other (Westergaard and Suomi 1997). Two capuchins also performed active transfers of tools between each other even though the recipient never returned a share of the reward to the donor (Westergaard et al. 2007).

In this study, we tested the ability of brown capuchin monkeys and Tonkean macaques to reciprocate in a task requiring two subjects to exchange tokens in order to obtain rewards from an experimenter. By monitoring the occurrence of transfers, the value of goods exchanged and the alternation of roles between individuals, we aimed at assessing the extent to which monkeys may purposefully engage in reciprocal behaviors with conspecifics.

Methods

Subjects

We tested 4 brown capuchin monkeys (*Cebus apella*) and 3 Tonkean macaques (*Macaca tonkeana*) maintained at the Primatology Centre of the University of Strasbourg, France. Table 1 presents the age and sex of individuals. Subjects lived in social groups housed in enclosures with access to indoor and outdoor areas. Water was available ad libitum and subjects were never food deprived. Subjects of both species had been involved in food-exchange tasks with humans prior to this study (Drapier et al. 2005; Pelé et al. 2010a) but never in a token-exchange task involving a conspecific.

Tokens

We used three kinds of tokens differing in shape, material and color for the exchange task (pink PVC caps, wooden cubes and metallic nuts). The tokens used with the capuchins were smaller than those used with the macaques (2 cm vs. 4 cm in length) to compensate for the hand size of each species.

For each pair of subjects, we gave to both partners the same set of 36 tokens composed by three types of 12 tokens: (1) *Self-valued tokens* were valuable to the subject and valueless to the partner; (2) *Partner-valued tokens* were valuable to the partner and valueless to the subject; (3) *No-value tokens* were not valuable for any partner. Table 1 gives information about the self-valued tokens of each subject.

Training procedure

Subjects were trained individually to exchange one of the three types of tokens for food in one compartment of the testing room. The experimenter (M.P.) sat in front of the subject and placed the 36 tokens in the compartment. Subject and experimenter could give and receive tokens through the wire-meshed fence of the enclosure. A session

Table 1 Age and sex of subjects, and types of self-valued tokens

Name	Species	Age (years)	Sex	Self-valued tokens
Arn	*Cebus apella*	10	Male	Metallic nut
Kin	*Cebus apella*	17	Female	Metallic nut
Pis	*Cebus apella*	7	Male	Pink PVC cap
Pop	*Cebus apella*	7	Male	Wooden cube
Rim	*Macaca tonkeana*	6	Male	Wooden cube
She	*Macaca tonkeana*	5	Male	Metallic nut
Syb	*Macaca tonkeana*	5	Female	Pink PVC cap

typically started with the experimenter requesting tokens by holding an open hand (palm up) next to the fence. The experimenter only rewarded (with a piece of banana) the transfer of subject-valued tokens. All other tokens were accepted by the experimenter (and dropped on a bucket), but no reward was given in return. Once the subject had returned his/her 12 self-valued tokens, the experimenter ended the session. Subjects of both species advanced to the testing phase upon giving more than 90% of the correct tokens first during three consecutive sessions.

Testing procedure

Testing took place in the same testing room divided into two compartments by a common wired-mesh fence (Fig. 1). The mesh allowed subjects to see their partner moving in their compartment or exchanging tokens with the experimenter. We chose pairs of individuals according to their social relationships; only those being able to contact each other affiliatively and to eat at close proximity were qualified for the study. Three pairs were tested in each species (capuchins: Arn*/Pis, Pis*/Pop, Kin/Pis*; macaques: Rim*/Syb, Rim*/She, She/Syb*). Asterisks indicate the higher-ranking individual in each pair; dominance relationships were assessed by the direction of the supplantations induced by a fruit juice competition test (see Thierry et al. 1994). Twelve tests were run for each pair of individuals. Only 10 tests could be conducted in one pair of capuchins (Arn/Pis) because of difficulties in selecting the individuals.

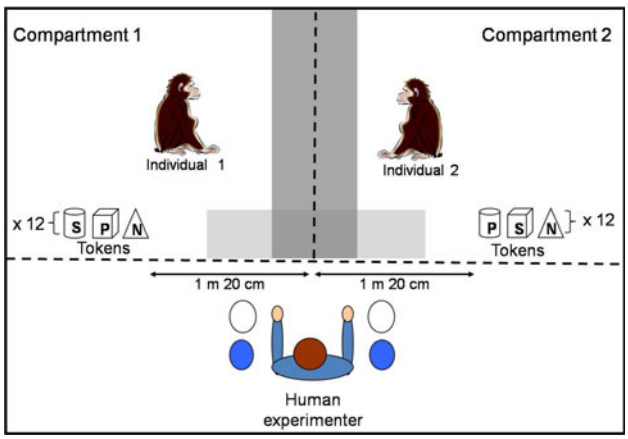

Fig. 1 Experimental setting: two subjects are placed in adjacent compartments separated by a common mesh (*dotted lines*). Both partners receive the same set of tokens: 12 self-valued tokens (S), 12 partner-valued tokens (P) and 12 no-value tokens (N). Tokens are placed 1 m 20 cm away from the common mesh, out of partner's reach. Tokens can be transferred by passing them through the common mesh. Two areas have been defined: the experimenter exchange area (*light grey shaded box*) in which subjects exchange tokens with the experimenter, and the common mesh area (*dark grey shded box*) corresponding to the area within reach of the partner through the mesh (20 cm of length for capuchins, 40 cm of length for macaques)

The testing procedure was the same as the training one except that two individuals were present in each of two adjacent compartments. The experimenter placed the same set of 36 tokens (12 self-valued tokens, 12 partner-valued tokens and 12 no-value tokens) in each compartment, near the experimenter exchange area and 1 m 20 cm away from the common mesh, out of partner's reach. Once both subjects had entered their testing compartment, the experimenter sat facing the common mesh to be at equal distance of both compartments. She sat with her hands on her lap in a relax position and resumed that position after an exchange has occurred. Whenever a subject picked up a token and inserted her/his hand trough the mesh toward the experimenter, she opened her hand offering the subject to exchange it. This procedure was followed regardless of the type of token held by the subjects. When both subjects attempted to exchange at the same time, the experimenter used both hands (the token was received with the left hand and the reward given with the left hand—when appropriate—for the subject in the left compartment, and the same sequence was performed with the right hand for the subject placed in the right compartment). Only self-value tokens were rewarded by a piece of food, other tokens were discarded in a small bucket in front of the experimenter without being rewarded. Then, the experimenter resumed the relax position while reporting the subject, type of token given and time of exchange, visible on the chronometer on the floor. In addition, the experimenter never directly looked at the tokens or at the subjects to avoid influencing their behaviors.

In the first part of each test, partners had the opportunity to exchange their self-valued tokens with the experimenter against a piece of banana. The experimenter accepted all other tokens from the subjects, but they received no reward in return. Once both individuals have given all their 12 self-valued tokens, the experimenter faced the partners for a time period of 10 min. At this stage, only partner-valued tokens and no-value tokens remained in each compartment. If transfers of valuable tokens occurred, the experimenter asked for it by holding her hand palm up and exchanged it for food with the subject.

During testing sessions, the experimenter recorded different behavioral units using a handheld recorder placed on a support at voice-level of the experimenter: *Exchange with experimenter*: A subject passes a token through the mesh to the experimenter. *Transfer with partner*: A recipient obtains a token that was originally in the compartment of her/his partner. The frequency, latency and token value of these two behaviors were scored. The experimenter also recorded the type of transfer: *Passive transfer*: A recipient obtains a token by sizing it in the partner's enclosure. At the beginning of the trial, tokens of a partner are not within

reach of the recipient. Therefore, passive transfers can result from a placement with the hand near the common mesh (within reach of the partner), or from an accidental displacement (after being dropped, stepped on or pushed the token ends up near the common mesh, within reach of the partner). The experimenter recorded whether passive transfers occurred after accidental interaction or placement by the partner. *Active transfer*: A subject places a token in the compartment, the hand or mouth of her/his partner. Finally, the experimenter recorded the frequency and the identities of actor and recipient of potential begging behaviors such as vocalizations, facial mimics or gestures (for instance, *holding out hand* when a subject holds one hand with the palm up in the partner's direction).

Statistical analyses

We used Chi-square tests to compare types of tokens exchanged, Wilcoxon matched-pairs tests to compare frequencies of exchanges, transfers and manipulations by each individual using the exact test procedure on SPSS 16© (Siegel and Castellan 1988; Mundry and Fischer 1998) and the Fisher method for combining probabilities from independent tests of significance (Sokal and Rohlf 1969). The significance level was set at 0.05. Average values are given as mean and SEM.

Results

Exchanges with the experimenter

In the training phase, capuchin monkeys needed on average 10.3 ± 1.0 sessions to discriminate (i.e., preferentially exchange) their self-valued tokens from others, whereas Tonkean macaques needed 15.3 ± 3.7 sessions. We checked whether subjects showed a preference for one type of token by comparing the 12 first given tokens at the first training session to an equal distribution of tokens. No significant difference was found for one of the three types of token in any subjects (Chi-square test). During the testing phase, each test started with individuals exchanging their 12 self-valued tokens with the human experimenter. As a mean, the 12 first given tokens were composed of 11.2 ± 0.1 self-valuable tokens in capuchins, and of 11.7 ± 0.1 self-valuable tokens in macaques. The whole set of self-valued tokens was exchanged in a mean of 416 ± 33 s for capuchins and in a mean of 268 ± 15 s for macaques. Figure 2 presents the mean number of valueless tokens, including both partner-valued and no-value tokens, which were given to the experimenter by each subject (statistical values are also provided in ESM). When comparing the value of the tokens given, two capuchins

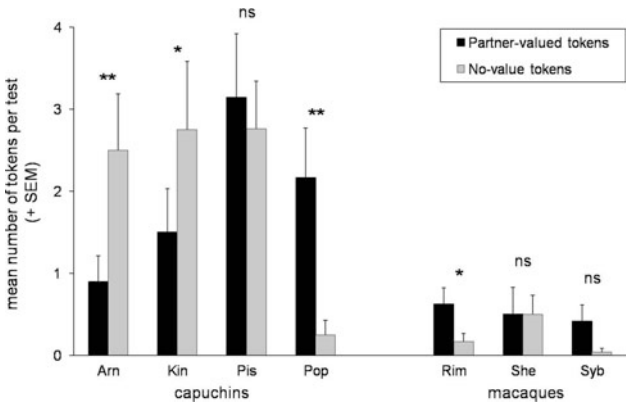

Fig. 2 Number of valueless tokens (partner-valued and no-value tokens) given to the experimenter by each subject (Wilcoxon test, one tailed, * $P < 0.05$, ** $P < 0.01$)

(Arn, Kin) gave significantly more no-value tokens than partner-valued tokens to the experimenter. On the contrary, one capuchin (Pop) and one macaque (Rim) gave significantly more partner-valued tokens than no-value tokens to the experimenter.

Transfer with partner

We recorded 56 transfers in capuchins (1.64 transfers per test) and 10 transfers in macaques (0.27 transfers per test). In both species, all transfers recorded were passive, i.e., all tokens transferred were taken by the subject from the compartment of the partner (see ESM). In both species, tokens transferred ended up near the common mesh by accidental displacement (after being manipulated—i.e., handled, or put in mouth- and then dropped, stepped on or pushed). Consequently, we analyzed whether individuals manipulated those tokens that were valuable for the partner closer to the common mesh as opposed to those that were not. Figure 3 presents the mean number of tokens brought

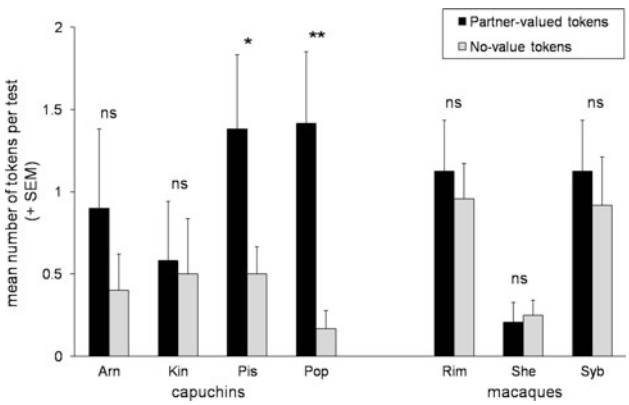

Fig. 3 Number of valueless tokens (partner-valued and no-value tokens) manipulated by subjects and ending up near the common mesh (Wilcoxon test, one tailed, * $P < 0.05$, ** $P < 0.01$)

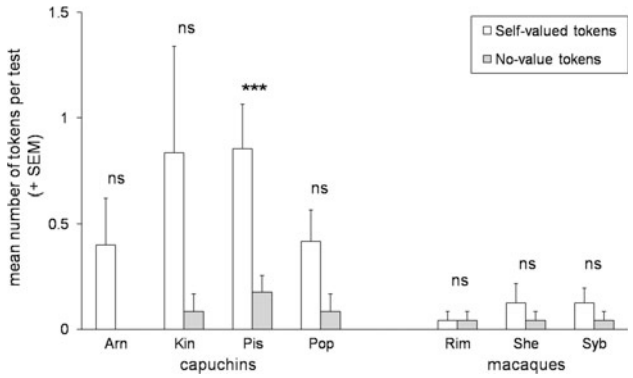

Fig. 4 Number of self- and no-value tokens taken by subjects from their partner's compartment (Wilcoxon test, one tailed, *** $P < 0.001$)

to and manipulated near the common mesh by each individual (statistical values are also provided in ESM). Two capuchins (Pis, Pop) manipulated significantly more partner-valued tokens than no-value tokens near the common mesh. The other two capuchins did not show a significant difference in manipulation, but their performances went in the same direction; so, we combined the probabilities using the Fisher method (Sokal and Rohlf 1969). Capuchins manipulated significantly more partner-valuable tokens than non-valuable ones near the mesh (Fisher test, $\chi^2 = 23.6$, $df = 8$, $P < 0.01$).

Not surprisingly, valuable tokens represented 86% of the tokens taken by capuchins and 70% of the tokens taken by macaques from their partner's compartment (Fig. 4 and ESM). One capuchin (Pis) took significantly more self-valuable tokens than non-valuable ones from the compartment of his partner. The other three capuchins did not show a significant difference in the value of tokens taken, but they showed the same average pattern; so, we combined their probabilities using the Fisher method (Sokal and Rohlf 1969). Capuchins took significantly more self-valuable tokens than non-valuable ones from the compartment of their partner (Fisher test, $\chi^2 = 29.1$, $df = 8$, $P < 0.001$).

Discussion

Both Tonkean macaques and brown capuchin monkeys learned to discriminate their own valuable token among three different types, as shown by their preferential choice of those tokens to exchange with the experimenter. This result confirms that monkeys form associations between tokens and food rewards (Westergaard et al. 1998; Brosnan and de Waal 2004a). However, no active transfers of tokens were observed between partners. Instead, we recorded a number of passive transfers, especially in capuchin monkeys, that were enabled by the displacement of tokens toward the common mesh.

Capuchins learned to pick up tokens valuable for them from their partner's compartment. One capuchin (Pis) was even observed frequently walking back and forth along the common mesh while monitoring tokens almost within reach. Interestingly, partners displaced a greater proportion of partner-valuable tokens than no-valuable tokens near the common mesh. Because one individual (Pis) was tested in every pair, it may be argued that he had a prominent role in this outcome. To control for this, the partner-valued tokens differed depending on the partner he was associated with. In addition, other subjects also displaced partner-valued tokens. Thus, our results cannot be attributed to a single individual, even if caution remains advisable regarding any extension of them. This differential displacement cannot be attributed to a greater propensity to exchange partner-valued than no-value tokens with the experimenter because they exchanged both types with an equally and low proportion. Although the displacement of one type of token could have been done purposefully, the absence of active transfers makes it difficult to evaluate whether partners purposefully manipulated the tokens valuable to their partners near the common mesh so that they could benefit from them.

The absence of active transfers between subjects in Tonkean macaques and brown capuchin differs from some previous observations of active gifts from one individual to another in capuchins (de Waal et al. 1993; de Waal 1997; Westergaard and Suomi 1997; Westergaard et al. 2007). A parsimonious hypothesis is that the potential roles of receiver and donor in our experiment have not been understood by subjects. As receivers, subjects must understand that their partner is instrumental in providing more tokens. This could be expressed by individuals through solicitation or the use of begging behaviors such as pointing and holding-out-hand gestures as observed in great apes (Pelé et al. 2009; Yamamoto and Tanaka 2009). In monkeys, brown capuchins have been observed putting cupped hands under the mouth of conspecifics to pick up falling pieces of food which might be interpreted as solicitation gestures (de Waal et al. 1993). In our study, however, neither capuchin monkeys nor Tonkean macaques performed such begging gestures toward their partner.

The lack of solicitations may have further made individuals less inclined to act as donors. We never observed our subjects giving a token to their partner. At present, there is no evidence that monkeys can recognize the interests of others (Barnes et al. 2008). In our study, both no-value and partner-valued tokens had never been reinforced by the experimenter, but capuchins appeared to manipulate the partner-valued tokens more often than the no-value ones, leading to more opportunities for these

tokens to end up near the common fence within reach of the partner. While passive, transfers of tokens could be facilitated by the initial possessor as previously reported in a pair of orangutans (Dufour et al. 2009), but we never observed a monkey actually 'placing' a token within reach of the partner. Alternatively, by watching their partner successfully exchanging their token for food, subjects may have attributed more value to those tokens than to the no-value ones and thus manipulated them more. Indeed, capuchin monkeys can learn the value of different tokens by watching others exchanging tokens for food (Brosnan and de Waal 2004b). Although the setup gave visual access to the subjects, allowing them to learn about the value of their partner's tokens (Dufour et al. 2009), we cannot definitively conclude that they did so in the present study. Further experiments should be run to assess the extent to which this may have affected our results. If the subjects did learn something about the value of the tokens, it remains that they did not attempt to exchange them with the experimenter.

In humans, trust is commonly viewed as a 'lubricant' of economical transactions (Arrow 1974). It could be as well a critical component of reciprocal interactions in non-human primates. While an individual can be flexible enough to tolerate occasional defection from a partner, he/she still needs some assurance that there is a potential for favors to be returned (Pelé et al. submitted). Such expectations may not be strong enough in macaques and capuchins, even preventing individuals to initially invest by giving first to their partners. By comparison, results from a similar experiment run with four great ape species showed that at least one individual in each species actively took the first step (Pelé et al. 2009). Here, none of the pairs tested engaged in short-term reciprocal interactions, despite optimal conditions where values of goods were defined and could be learned by partners, even in subjects having been repeatedly tested with different partners. These results indicate that calculated exchange is difficult if not impossible between monkeys. Further studies in a larger number of individuals and species will be necessary to verify the accuracy of this conclusion.

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