

# Evaluation of third-party reciprocity by squirrel monkeys (*Saimiri sciureus*) and the question of mechanisms

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**Abstract** Social evaluation during third-party interactions emerges early in human ontogeny, and it has been shown in adult capuchin monkeys who witness violations of reciprocity in object exchanges: Monkeys were less inclined to accept food from humans who refused to reciprocate with another human. A recent study reporting similar evidence in marmoset monkeys raised the possibility that such evaluations might be based on species' inherent cooperativeness. We tested a species not renowned for cooperativeness—squirrel monkeys—using the procedure used with marmosets and found a similar result. This finding rules out any crucial role for cooperative tendencies in monkeys' responses to unfair exchanges. We then tested squirrel monkeys using procedures more similar to those used in the original study with capuchins. Squirrel monkeys again accepted food less frequently from non-reciprocators, but unlike capuchins, they also strongly preferred reciprocators. We conclude that neither squirrel monkeys nor marmoset monkeys engaged in emotional bookkeeping of the type that probably underlies social evaluation in capuchin monkeys; instead, they employed one or more simple behavioral rules. Further comparative studies are required to clarify the mechanisms underlying social evaluation processes across species.

**Keywords** Non-human primates · *Saimiri sciureus* · Social exchange · Third-party relationships · Reciprocity · Social evaluation

## Introduction

As in a wide range of animal species (Earley 2010), eavesdropping on social interactions between third parties is common in non-human primates (Cheney 2011). The advantages of eavesdropping for monkeys and apes include acquisition of information about mating opportunities (Crockford et al. 2007), others' competitive abilities or social dominance (Borgeaud et al. 2013; Cheney et al. 1995), or foraging opportunities (Russell et al. 2008; Subiaul et al. 2008). In the latter studies, for example, chimpanzees eventually learned to beg preferentially from a 'generous' human actor who shared food with a third party (beggar), rather than a 'mean' actor who refused to share.

With the possible exception of studies on inequity aversion (for review, see Brosnan and de Waal 2014), studies of non-human primates' social evaluations of individuals based on third-party interactions are rarely conducted from the perspective of moral judgments or perceptions of fairness. This latter perspective is more typical of studies with humans; moral behavior, including fairness in exchanges of resources, is considered crucial for cooperative societies to function effectively (Alexander 1987; Sun 2013). Signs of moral reasoning emerge early in human infants. For example, before 2 years of age, infants evaluate the fairness of distributions of items such as food or toys between third parties, expressing negative or surprise reactions when individuals benefit from inequitable sharing (Geraci and Surian 2011; Schmitt and Sommerville 2011; Sloane et al. 2012).

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Comparative cognitive scientists have asked whether non-human species—particularly other primates—are sensitive to violations of fairness. Alongside studies in which two monkeys or apes receive different rewards for performing the same task (Brosnan and de Waal 2014), recent studies have examined how monkeys respond to unfair exchanges between third parties. Do such violations influence the monkeys' social evaluations of the actors? Anderson et al. (2013a) showed that capuchin monkeys were less willing to accept food from human actors who consistently failed to reciprocate in exchanges compared to actors who did reciprocate, providing clear evidence of non-food-related image scoring in a non-human species.

Capuchin monkeys show well-documented prosocial tendencies and cooperativeness (deWaal et al. 2008; Sabbatini et al. 2012; Takimoto et al. 2010), so it may be asked whether these tendencies are crucial to their sensitivity to reciprocity violations. This hypothesis was tested in a recent study on another New World monkey species, the common marmoset. Marmosets are characterized by a cooperative breeding system in which several individuals take care of offspring (Snowdon and Ziegler 2007). Individual marmosets were reported to accept food less frequently from a human non-reciprocator than a reciprocator in a variant of the exchange situation used with capuchins (Kawai et al. 2014). The question then arises: Is this a case of convergent evolution in two species that show within-group cooperation, or is third-party-based social evaluation a more general primate trait?

In the present study, we asked whether squirrel monkeys—a New World monkey species not renowned for cooperating—also socially evaluate humans in the context of third-party object exchanges. Although squirrel monkeys sometimes cooperate with members of their group to defend resources, gain access to sexual partners, or mob predators (Boinski and Mitchell 1994), they do not help in the rearing of other individuals' offspring as marmosets do, and there are no reports of squirrel monkeys cooperating to solve instrumental tasks as described in capuchins and marmosets (Mendres and de Waal 2000; Werdenich and Huber 2002). We first tested squirrel monkeys in a variant of the exchange procedure recently used with marmosets (Kawai et al. 2014) and then tested them using a procedure more similar to that used with capuchins (Anderson et al. 2013a). In view of the relative lack of evidence for cooperativeness or prosociality in squirrel monkeys, we predicted that, unlike capuchins and marmosets, they would show no sensitivity to violations of reciprocity in exchanges between third parties.

## Experiment 1

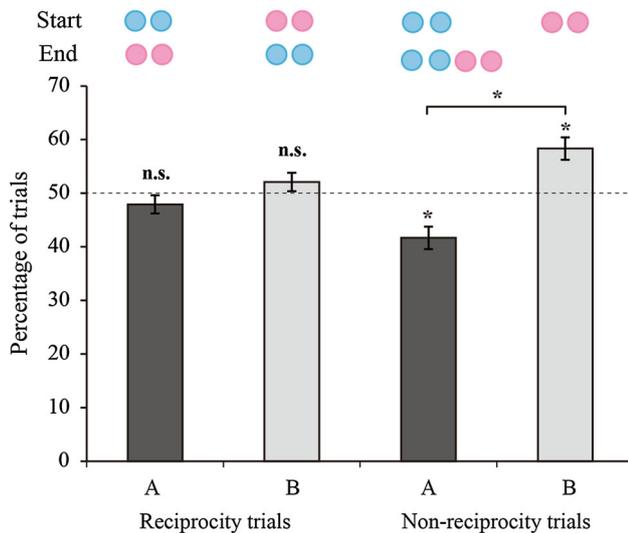
### Methods

#### *Subjects*

Six group-reared adult squirrel monkeys (*Saimiri sciureus*), two males and four females, participated. The monkeys were housed in a multi-level cage complex either in groups ( $N = 4$ ) or individually ( $N = 2$ ) with close visual and auditory contact with neighboring monkeys. They received food in their home cages every morning and afternoon (foods included commercial primate pellets, fruits, vegetables, egg), with water available ad libitum. All had experience of the room in which the study was conducted, but before the study started, each was given up to four daily familiarization sessions of 10 min in the test cage in the room, where they received several food treats. They were previously trained to enter a transport box in which they were transferred to the test cage. Housing and care of the monkeys adhered to Kyoto University Primate Research Institute's *Guide for the Care and Use of Laboratory Primates* (2nd ed.). The experimental procedures received approval from the Animal Experiment Committee of the Graduate School of Letters, Kyoto University.

#### *Apparatus and procedure*

On every trial, two adult male humans (actors "A" and "B"), familiar to the monkeys, sat side by side at a table about 50 cm in front of the subject, and 25 cm apart. Two small balls—pink for one actor, blue for the other—lay on the table in front of each actor. To start a trial, an opaque screen that blocked the monkey's view of the table and actors was removed. When *B* saw that the monkey was facing forward, he picked up his two balls one by one and placed them on the palm of his other hand, which he then moved toward actor *A*. The latter responded by taking each ball from *B*'s hand and placing it on the table, beside his own balls. In "reciprocity" trials, *A* then likewise placed his two balls in the palm of one hand and presented them to *B*; the latter took the balls and placed them on the table so that at the end of the trial each actor possessed the other's original two balls. By contrast, in "non-reciprocity" trials, *A* responded to *B*'s attempt to remove the balls from his hand by briefly turning his head away twice while making a blocking gesture, and then simply picking up his two balls one by one and returning them to the table. Thus, at the end of non-reciprocity trials, *A* had all four balls, whereas *B* had none. The start and end states of the balls in each condition are illustrated in Fig. 1



**Fig. 1** Start and end states of balls, and mean percentage of trials (+SE) in which monkeys accepted food from actors *A* and *B* in experiment 1

(see also supplementary movies 1 and 2). Each manipulation of a ball took approximately 1 s. During their interaction, the actors remained silent and focused only on the balls, making no eye contact with each other or with the monkey.

After the interaction, the opaque screen was reinstated and the balls were removed from the table. Approximately 5 s later, the screen was removed again to reveal each actor holding an identical piece of food between the index finger and thumb of one hand. Slowly and simultaneously, each actor moved the food toward the monkey and placed it on a mark 12 cm from the test cage and 18 cm apart. Each actor then placed his hand palm down 2 cm behind the food to maintain the association between specific actor and food offered. Throughout, the actors fixated a spot on the table between and in front of the two pieces of food. The food offered varied according to the monkeys' individual preferences known from daily feeding and previous experiments and included pellets, pieces of peanut, apple, banana, sweet potato, and raisins. The monkey chose one item by reaching for it through a 3-cm-high gap that ran along the front of the test cage. When this happened, the actor whose food was chosen simply withdrew his hand, while the other actor picked up his food item before withdrawing his hand. The screen was then reinstated, and the inter-trial interval (ITI) began. ITIs lasted approximately 10 s, during which the next trial was prepared, including the actors changing positions if required by the pseudo-randomized schedule in which no more than two consecutive identical trials were permitted. Each of the 12 sessions contained six reciprocity and six non-reciprocity trials. Every trial in the experiment was video-recorded

using a Sony HDD Handycam (Model No. DCR-SR220) mounted on a tripod and positioned between and slightly behind the two actors to provide an unobstructed view of the monkey. The two actors played the roles of *A* and *B* equally frequently across sessions.

### Data analysis

In view of the small sample size, nonparametric tests were used to analyze the monkeys' frequencies of accepting food from actors *A* and *B* compared to chance levels (Wilcoxon one-sample tests, exact version) and to compare the frequency of accepting food between the two actors (Wilcoxon signed-rank test, exact version) for both reciprocity and non-reciprocity conditions. For all analyses, alpha was set at 0.05.

### Results and discussion

In reciprocity trials, *A* and *B* were both selected at near-chance level (mean 34.5 and 37.5, respectively,  $Z = -1.48$ ,  $N = 6$ ,  $p = .14$ ), with no significant difference in frequency of choosing between them ( $Z = -1.26$ ,  $N = 6$ ,  $p = .21$ ). By contrast, in non-reciprocity sessions, *A* and *B* were consistently chosen less and more frequently than expected by chance (mean 30 and 42, respectively,  $Z = -2.0$ ,  $N = 6$ ,  $p = .046$ ), and the monkeys accepted food more frequently from actor *B* than from non-reciprocal actor *A* ( $Z = -2.03$ ,  $N = 6$ ,  $p = .046$ ) (see Fig. 1).

These results partially replicate those of a recent study in which marmosets were reported to show a diminished frequency of accepting food from an actor who had failed to reciprocate in an exchange of food with a third party (Kawai et al. 2014), even though the actors' interactions in the present study did not involve food. As squirrel monkeys are neither cooperative breeders nor notably prosocial, these results suggest a widespread distribution of sensitivity to reciprocity violations in New World monkeys, rather than a restricted distribution due to convergent evolution.

However, the following procedural differences between both the marmoset study and experiment 1, and the original study of capuchins (Anderson et al. 2013a) need to be considered: (1) In the study with capuchins, the exchange involved actors actively donating the items, whereas here (and in Kawai et al. 2014) the exchange involved taking objects from the other actor's hand. (2) In the capuchin study, non-reciprocity was signaled by a single look-away movement by the actor, whereas in experiment 1 and Kawai et al. (2014), the non-reciprocator looked away more than once and also made a push-away gesture (pers. comm. by N. Kawai, 08.05.2014). (3) In the capuchin

study, experimental sessions consisted of only one trial type (reciprocity or non-reciprocity), whereas in experiment 1 and Kawai et al. (2014), both types of trials were run in each session. We therefore conducted experiment 2 to see whether squirrel monkeys would show sensitivity to violations of reciprocity in a procedure more like that used in the study with capuchin monkeys (Anderson et al. 2013a).

## Experiment 2

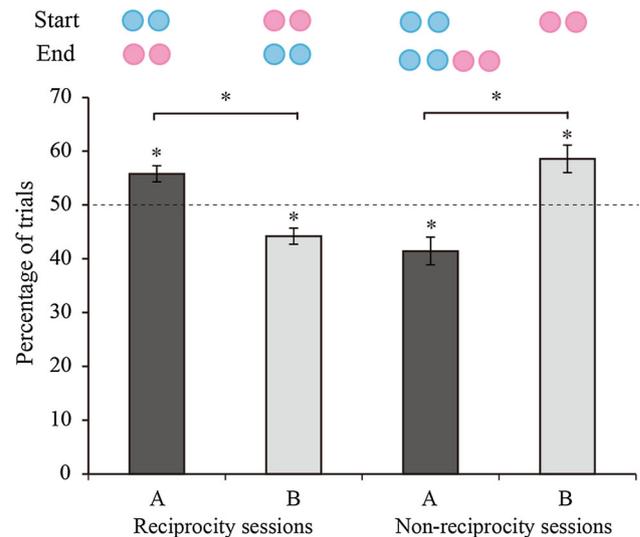
### Methods

#### Subjects

Six group-reared adult squirrel monkeys (*Saimiri sciureus*), two males and four females, participated. These monkeys were not those used in experiment 1, but they were housed and cared for similarly, and they were familiar with the actors, and experimental room and test cage, which were identical to those in experiment 1.

#### Apparatus and procedure

Each trial started with the opaque screen being removed to reveal the two actors (“A” and “B”) sitting side by side as in experiment 1. An empty transparent plastic container and two small balls (blue for one actor, pink for the other) lay on the table in front of each actor. Once the monkey was facing forward, A picked up and held out his empty container toward B to request the latter’s balls. B responded by picking up and transferring his 2 balls one by one to A’s container, which A then returned to the table. B then likewise requested A’s balls. In 50 % of sessions, A always reciprocated by transferring his own balls just as B had done (“reciprocity” sessions). In the other 50 % of sessions, A failed to reciprocate (“non-reciprocity” sessions), but responded instead by briefly turning his head away then simply lifting up each of his own balls in turn and returning it to the table. After these actions, B returned his empty container to the table; A thus ended up with all 4 balls, B with none (see Fig. 2, and supplementary movies 3 and 4). Each manipulation of a ball took approximately 1 s. During their interaction, the actors remained silent and focused on the balls and containers; they made no eye contact with each other or with the monkey. After each completed exchange or non-exchange, the screen was reinstated and the containers and balls removed from the table. The screen was then removed, and each actor offered a piece of food to the subject exactly as in experiment 1. Six reciprocity and six non-reciprocity sessions of 12 trials each were run in alternation, with the two actors playing



**Fig. 2** Start and end states of balls, and mean percentage of trials (+SE) in which monkeys accepted food from actors A and B in experiment 2

the roles of A and B equally frequently across sessions. The data were analyzed the same way as in experiment 1.

### Results and discussion

As in experiment 1, non-reciprocating A and actor B were chosen less and more frequently than chance, respectively (mean 29.8 and 42.2,  $Z = -2.0$ ,  $N = 6$ ,  $p = .046$ ). Unlike in experiment 1, however, reciprocal A was chosen more frequently than chance, with B consequently being selected less frequently than expected (mean 40 and 32, respectively,  $Z = -2.23$ ,  $N = 6$ ,  $p = .026$ ). In the reciprocity condition, the monkeys took food from actor A significantly more frequently than from actor B ( $Z = -2.23$ ,  $N = 6$ ,  $p = .026$ ), whereas in the non-reciprocity, the preference was reversed: Food offered by A was chosen less frequently than food offered by B ( $Z = 1.99$ ,  $N = 6$ ,  $p = .046$ ) (see Fig. 2).

These results indicate that squirrel monkeys resembled capuchin monkeys in terms of negative evaluation of third-party non-reciprocators, albeit with a simplified interaction—two balls exchanged instead of three, as in the previous study by Anderson et al. (2013a). Unlike capuchin monkeys, however, squirrel monkeys also showed a positive preference for actors who reciprocated. It would be of interest to know whether, like capuchin monkeys (Anderson et al. 2013a), squirrel monkeys would also be sensitive to (1) partial reciprocity violations as opposed to total non-reciprocity, and (2) the reason for failure to reciprocate, such as one actor starting out with fewer goods than the other actor. These conditions are described in more detail below.

## General discussion

In both experiments reported here, squirrel monkeys were found to negatively evaluate third-party non-reciprocators, both when the procedure used was like that used with marmosets by Kawai et al. (2014) and more like that used to study social evaluation in capuchin monkeys by Anderson et al. (2013a). Thus, our prediction that this relatively non-cooperative New World primate species would not show third-party-based social evaluation was not supported.

In experiment 1, squirrel monkeys showed similar behavior to the marmosets in Kawai et al. (2014) even though unlike in the study with marmosets, the exchange scenarios between the two actors concerned non-edible objects. This finding rules out the possibility that use of food was a contaminating factor in the marmoset study. However, the positive result for squirrel monkeys in experiment 1 also contradicts Kawai et al.'s (2014) suggestion that third-party-based image scoring stems from inherent cooperativeness, as squirrel monkeys are neither cooperative breeders nor notably prosocial in other contexts. In other words, high levels of cooperativeness or prosociality do not appear necessary for sensitivity to reciprocity violations in third-party exchanges. Alternatively, the positive results obtained in marmosets by Kawai et al. (2014) and in squirrel monkeys in experiment 1 might be attributable to the specific procedures used in those studies, notably the facts that (1) the behavior of the donor actor was relatively passive, consisting of simply allowing the other actor to take the objects out of his hand, and (2) the non-reciprocator's refusal to allow the transfer was more exaggerated than in Anderson et al. (2013a), incorporating repeated head movements away from the requesting actor and a manual blocking gesture.

Experiment 2 assessed squirrel monkeys' social evaluations using procedures much more similar to those used in the original study of capuchin monkeys (Anderson et al. 2013a): Actors exchanged by actively donating objects, non-reciprocity was signaled by a single look away with no other gesture, and experimental sessions consisted of one trial type only. In these conditions, squirrel monkeys again consistently discriminated against non-reciprocating actors. To this extent, they showed evidence of a negativity bias that may be shared with both human infants (Hamlin et al. 2010) and capuchin monkeys presented with not only unfair third-party exchanges, but also other types of anti-social interaction (see Anderson et al. 2013b). Importantly, however, unlike capuchin monkeys, squirrel monkeys also showed a preference for accepting food from a reciprocating actor. In other words, whereas capuchin monkeys showed only a consistent negative bias, squirrel monkeys

showed both negative (to the non-reciprocator) and positive (to the reciprocator) biases. This pattern suggests that the squirrel monkeys' strategy was simply to *choose the last actor to donate to the other actor*. This simple rule would account for their preference for actor B in non-reciprocity sessions and A in reciprocity sessions, and their preference for actor B in non-reciprocity trials in experiment 1. One or more of the other procedural differences between the two experiments might be the reason that the differential selection of either actor in the reciprocity condition was significant in experiment 2 only. That capuchin monkeys in Anderson et al. (2013a) did not rely on such a strategy was shown by conditions in which the non-reciprocator actively donated a smaller number of balls than she received.

It also seems important to note, in experiment 1 and Kawai et al.'s (2014) study, trial-to-trial variability in whether the exchange was reciprocal or not negated any need for cumulative emotional/affective bookkeeping of the two actors' behavioral tendencies as the session progressed. Instead, the monkeys could base their choice on every trial simply on the most recently witnessed interaction.

It would be of interest to test both marmosets and squirrel monkeys on further conditions such as *partial reciprocity*—actor A donates at least one item but less than she received—and *impoverished reciprocity*—actor A starts out with only one item which she donates after receiving a greater number. In partially reciprocal exchanges, if marmosets or squirrel monkeys tend to choose the last actor to donate, then they might be expected to show a preference for the non-reciprocator in this condition. Capuchin monkeys did not show such a preference; they continued to show a bias against the unfair actor. In impoverished reciprocity, capuchin monkeys showed no discrimination against an actor who donated fewer balls than she received because she had fewer balls to start with (Anderson et al. 2013a). This finding implies that capuchin monkeys take into account not only the end state of an exchange, but also the start state in terms of the relative “wealth” of the two actors. In the absence of information about how marmosets and squirrel monkeys respond in these additional conditions, it appears premature to conclude that their third-party-based social evaluations are equivalent to those seen in capuchin monkeys, or that they are based on the same mechanism of emotional (or “affective”) bookkeeping (Schino and Aureli 2009) as in capuchin monkeys.

In this context, it is noteworthy that unlike great apes, capuchins and macaque monkeys, and even domestic dogs and corvids, both callitrichids (the family to which marmosets belong) and squirrel monkeys have repeatedly

failed to show evidence of inequity aversion when a conspecific receives a better reward for performing the same task (Brosnan and de Waal 2014; Talbot et al. 2011). If inequity aversion and true social evaluation during third-party reciprocity failures depend on a common underlying mechanism for detecting inequity, then the possibility remains that these joint abilities have a more restricted phylogenetic distribution than some authors have suggested.

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