Marmoset monkeys evaluate third-party reciprocity

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Many non-human primates have been observed to reciprocate and to understand reciprocity in one-to-one social exchanges. A recent study demonstrated that capuchin monkeys are sensitive to both third-party reciprocity and violation of reciprocity; however, whether this sensitivity is a function of general intelligence, evidenced by their larger brain size relative to other primates, remains unclear. We hypothesized that highly pro-social primates, even with a relatively smaller brain, would be sensitive to others’ reciprocity. Here, we show that common marmosets discriminated between human actors who reciprocated in social exchanges with others and those who did not. Monkeys accepted rewards less frequently from non-reciprocators than they did from reciprocators when the non-reciprocators had retained all food items, but they accepted rewards from both actors equally when they had observed reciprocal exchange between the actors. These results suggest that mechanisms to detect unfair reciprocity in third-party social exchanges do not require domain-general higher cognitive ability based on proportionally larger brains, but rather emerge from the cooperative and pro-social tendencies of species, and thereby suggest this ability evolved in multiple primate lineages.

1. Introduction

Reciprocity and cooperation are fundamental to human society [1] and are often observed in non-human primates. Although reciprocity is a type of altruistic behaviour, individuals expect a return based on their own actions towards a recipient. If the recipient fails to offer the provider of resources (e.g. food) or services (e.g. grooming) reciprocal resources, then punishment by the provider ensues [2]. If an individual repeatedly fails to reciprocate, then the opportunity to be a potential exchange partner will be lost. However, reciprocity requires the memory of actions, which is highly costly. In a recent study, capuchin monkeys observed reciprocal and non-reciprocal exchanges by human actors and accepted food less frequently from non-reciprocal actors than they did from reciprocal actors [3]. Although the capuchins’ social evaluations are explained [3, p. 144] as ‘cognitive adaptations underlying effective social exchange that have evolved in non-human primates [4], and these adaptations include sensitivity to non-reciprocity in the context of exchanges between third parties’, the evolutionary conditions that drive capuchin monkeys’ sensitivity with respect to the detection of non-reciprocal behaviour in third-party social exchanges are unknown.

One possibility is that the capuchin’s proportionally larger brain [5] facilitates higher cognitive ability in both social and non-social domains, enabling the monkeys to remember unbalanced reciprocity between third parties [3]. Brain size is generally associated with cognitive performance [5]. Capuchin monkeys show complex tool use in the wild [6] and superior performance on laboratory memory tasks [7].

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Another possibility is that capuchins’ performance is attributable to their social cognitive skills rather than their general intelligence [8]. Several hypotheses propose that cooperative breeding leads to increased cognitive ability, especially in social domains [9]. We hypothesized that a highly social and cooperative primate species, but relatively smaller brain size [5] and poor performance in non-social tasks, would show similar discrimination between reciprocal and non-reciprocal third-party social exchange. We tested marmosets using the same paradigm used to test capuchin monkeys [3] to assess the evolutionary conditions necessary for pronounced sensitivity to third-party reciprocity. This paradigm was chosen because marmosets outperform their sister taxa in socio-cognitive [10] rather than non-social domains [9], including working memory tasks [11]. We predicted that marmosets would express a preference for individuals who behaved reciprocally, as capuchins did. If marmosets preferred to accept food from third-party reciprocators, showing bias against non-recipients, then a proportionally larger brain size and better working memory are not necessary for this socio-cognitive skill; rather, pro-social traits common to two phylogenetically distinct families of New World monkeys would favour the evolution of social evaluation of third parties.

2. Material and methods

Four juvenile common marmosets (Callithrix jacchus, two males and two females) ranging in age from 1.5 to 2.0 years were housed individually in cages (51 × 31 × 61 cm). Marmosets lived with their families until 1.5 years old, then (after 1.5 years) they were kept individually. They had free access to water and were fed twice daily on a diet of monkey chow, supplemental vitamins and vegetables. They were tested using a small test apparatus (25 × 20 × 18.5 cm) with wire-walls in an experimental room at the National Center of Neurology and Psychiatry (NCNP) in Japan. Our study complied with current Japanese law and the guidelines approved by the Animal Experiment Committee of the NCNP.

During each trial, an opaque screen was opened to show the following scene to each monkey: two human actors (A and B) stood about 92 cm from the monkey and 50 cm apart. After confirming that the monkey’s attention was directed towards the actors, the demonstration began in accordance with one of two conditions. In either condition, two small pieces (1.5 cm³) of two types of food (a steamed bun and a potato) were placed on a table in front of each actor. These types of food were used to draw the monkey’s attention and to simulate a naturalistic situation, i.e. food sharing.

In the reciprocal condition, B first picked up two pieces of one type of food (e.g. potato). A then took the food from B and placed it near the non-transferred foods (i.e. bun). Following this, A picked up the non-transferred food, after which B took the food from A and placed it on the table. Thus, two pieces of food were exchanged between A and B. In the non-reciprocal condition, the initial transfer from B to A was the same as in the reciprocal condition. However, A refused to take the non-transferred foods from B and kept placing them back in their original position. Thus, A ended up with four pieces of food and B with none. The experimental set-up is depicted in the electronic supplementary material.

After the demonstration, the screen was closed and the food was hidden. Five seconds later, the screen was re-opened and each actor placed an edible reward (sponge cake) in front of the monkey; the pieces of food were placed 10 cm apart. When the monkey took one of the rewards, the screen was closed and the inter-trial interval of 10 s began. Two conditions were presented six times in one session. The combinations of foods, conditions and actors’ roles were counterbalanced within each session. These combinations were presented randomly over 12 trials in one session. The session was repeated six times.

The frequency of accepting food from A versus B was analysed using the exact variant of the Wilcoxon signed-rank test, as recommended for small sample sizes [12].

3. Results

In seven trials of a total of 576, two monkeys failed to take a reward from either actor. These seven trials were excluded from the analysis. In the reciprocal conditions, the monkeys’ preference for accepting the reward did not differ between actors (Z = −0.34, p = 0.77). By contrast, the monkeys exhibited a significant preference for actor B, the reciprocator, rather than actor A, the non-reciprocator (Z = −2.42, p = 0.014). The monkeys accepted food less frequently from actor A in the non-reciprocal condition than from actor A in the reciprocal condition (Z = 2.19, p = 0.028). The unbalanced exchange of food items between the actors led to a negative response towards non-reciprocator A in the subsequent choice. The raw data can be found in the electronic supplementary table.

4. Discussion

Results indicated that the marmosets responded negatively to non-reciprocal actors, even when they merely watched an unbalanced exchange between third parties who had no direct relevance to the monkeys and were not conspecifics, but humans. These findings are consistent with previous studies using capuchin monkeys [3] and human infants [13], with a number of important extensions.

First, the finding that marmosets (Callitrichidae) responded negatively to non-reciprocal behaviour between third parties indicates that this cognitive ability does not demand a proportionally larger brain [14] that enables the advanced cognitive
skills seen in capuchins [15] and chimpanzees [16]. Second, the monkeys in our study discriminated between non-conspecific reciprocators and non-reciprocators, despite the fact that this was their first experience of being in an experimental study involving human interaction. By contrast, the capuchin monkeys in Anderson et al.’s study had participated in experiments involving human interaction for years [3,14], suggesting that pronounced sensitivity to social exchange between human actors does not require learning to attend to human actors in an experimental setting. Rather, this ability seems to be present in some primate species. Third, the monkeys were sensitive to the roles of the reciprocator and the non-reciprocator, even when the roles were alternated quasi-randomly in the trials within a session, in contrast to the alternation performed in each session in the study using capuchins. Taken together, this study provides further evidence that some primate species, even in distinct phylogenetic families to capuchin monkeys, can perceive unbalanced reciprocity. This social evaluation is not specific to humans and does not require proportionally larger brain size, perspective-taking or language. This third-party social evaluation would be beneficial to species with respect to decision-making such as potential partners for cooperation.

Although similar third-party social evaluation was observed in phylogenetically different families (humans (Hominidae), capuchins (Cebidae) and marmosets (Callitrichidae)), whether this performance derived from homology or convergence related to socio-cognitive ability remains unclear. One may predict that sensitivity to reciprocity between third parties is widespread in primates (i.e. homology) because reciprocal grooming is an essential behaviour for most primates. If this were the case, then the origins of this ability would predate the divergence of New World and Old World monkeys [3], and other primate species should show similar sensitivity in third-party social evaluation. So far, empirical evidence is not available for species other than capuchin and marmosets.

Another account of the similar performance demonstrated by these three species posits that this performance occurs as a result of convergent processes arising from common environmental/social conditions. To be sensitive to third-party reciprocity, animals must understand that the exchange between others is unbalanced. We assumed that this sensitivity to unbalanced exchange relates to a sense of fairness [17]. Several primates are said to have a sense of fairness. When chimpanzees [18] and capuchin monkeys [18] were offered a lower value reward than their partners, they refused to accept it. However, there is no evidence of this in orangutans [19], which have proportionally larger brains, or squirrel monkeys [20] or tamarins [21]; species that are in the same phylogenetic family as marmosets. This non-systematic evidence for inequity aversion in primates suggests convergent evolution linked to cooperation [20]. We predict that primate species which understand third-party, non-reciprocal exchange should show inequity aversion, whereas primate species that are not concerned about receiving a lower value of reward than others will not be concerned about the unbalanced outcome of others’ social exchange. In fact, all species (humans, capuchins and marmosets) exhibiting negative responses to unbalanced reciprocity between third parties show inequity aversion [10,17,18], suggesting that their performance is derived from similar roots.

Given the non-systematic distribution of inequity aversion in primates [21] and marmosets’ poor performance in non-social tasks, third-party social evaluation seems to have evolved independently within Callitrichidae. Although the exact conditions required for this remain unclear, future studies should investigate whether a primate species that does not show inequity aversion can discriminate between reciprocal and non-reciprocal behaviour between third parties. Third-party social evaluation should be tested in large-brained, solitary non-human primates.

Our study complied with current Japanese law and the guidelines approved by the Animal Experiment Committee of the NCNP.


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References


