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Malini C. Suchak Date

Capuchin Monkeys Cooperate with Strangers:

Learning the Benefits of Reciprocity with In-Group and Out-Group Members

By

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Master of Arts

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Master of Arts

in Psychology

2010

Abstract
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By Malini Suchak

Humans are thought to be the only species capable of widespread cooperation with unrelated individuals. The purpose of this study was to determine if learned reciprocity facilitates cooperation in situations where cooperation normally breaks down in nonhuman primates: inequity aversion and among strangers. Twelve brown capuchin monkeys (*Cebus apella*) were tested to determine if they could learn the benefits of reciprocal exchange in a prosocial choice task. Capuchins did not develop contingent reciprocity in this task. Instead, mutualism led to an increase in prosocial behavior during reciprocal situations. Furthermore, capuchins overcame inequity aversion through reciprocity and demonstrated widespread cooperation with unfamiliar monkeys. These results demonstrate that (1) simple cognitive mechanisms can lead to increased cooperation and (2) cooperation outside the social group is not limited to humans.

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Introduction

Unlike any other species, humans cooperate with non-kin in large groups.

(Boyd, et al., 2003).

Human cooperation is a result of human capacities that are unique to our species.

(Bowles & Gintis, 2003).

The uniqueness of human cooperation has been the subject of much discussion in the literature. According to one view, humans are the only species to possess a trait known as strong reciprocity, which allows us to cooperate with unrelated individuals even when the potential for repayment is low (Bowles & Gintis, 2003; Gintis, 2000). Thus, a strong reciprocator is perfectly willing to cooperate with a complete stranger in a one-shot interaction. Whereas this type of behavior is commonly seen in human societies, there is little evidence for it in nonhuman animals.

On a proximate level, strong reciprocity is characterized by both a predisposition to cooperate with others (known as prosocial tendencies) and a predisposition to punish those who do not cooperate, even at a cost to oneself (Bowles & Gintis, 2003; Fehr & Fischbacher, 2003). The human uniqueness claim in this regard was initially supported by absence of evidence for prosocial tendencies in chimpanzees (Jensen et al., 2006; Silk et al., 2005; Vonk et al., 2008), but other studies have now demonstrated prosocial tendencies in both monkeys (Burkart, Fehr, Efferson & van Schaik, 2007; de Waal, Leimgruber & Greenberg, 2008; Lakshminarayanan & Santos, 2008) and apes (Hare & Kwetuenda, 2010; Warneken, Hare, Melis, Hanus, & Tomasello, 2007). In some of these situations (e.g. Hare & Kwetuenda, 2010; Lakshminarayanan & Santos, 2008) there was

an actual cost to benefiting the other. For the second characteristic of strong reciprocity, costly punishment, there are as yet no indications in other primates, suggesting the possibility of human uniqueness (Boyd, Gintis, Bowles & Richerson, 2003; Jensen, Call & Tomasello, 2007).

Despite the experimental evidence for prosocial tendencies in other primates, and the overwhelming support for same tendencies from naturalistic observations (Boesch & Boesch-Achermann, 2000; Goodall, J., 1986), the current view is that strong reciprocity is a uniquely human trait (Bowles & Gintis, 2003; Gintis, 2000; Fehr & Fischbacher, 2003). Theorists in support of this view argue that the evolution of strong reciprocity cannot merely be explained by kin-selection and reciprocal altruism, as these common explanations for cooperation in other species rely on relatedness and repeated interactions. Strong reciprocity is costly for the individual, but adaptive for the group. Therefore, multilevel group and cultural selection allow the norms of altruistic rewarding and punishment to be passed down through the population (Boyd et al., 2003; Fehr & Fischbacher, 2003). However, opponents of this viewpoint argue that strong reciprocity evolved from reciprocity, reputation (e.g. having a reputation as a "cooperator" is likely to cause others to cooperate with an individual in the future), and signaling, all self-interested traits that were individually selected (Akçay, van Cleve, Feldman, & Roughgarden, 2009; Burnham & Johnson, 2005). These mechanisms, already in place for repeated interactions and cooperation with kin and affiliates, create a predisposition to cooperate which simply extends to one-shot interactions with strangers. Thus, there are two areas of debate within the strong reciprocity literature: (1) whether or not strong reciprocity is uniquely human and (2) how it evolved.

Reciprocity in Nonhuman Species

Although some components of strong reciprocity may be uniquely human, the claim that humans are the only species to cooperate with non-relatives has been refuted by the primate literature. In fact, reciprocal exchange with non-relatives has been demonstrated extensively in our closest relatives, the chimpanzees (de Waal, 1997a; Koyama, Caws & Aureli, 2006). DNA analysis of chimpanzees in the field has confirmed widespread cooperation among non-relatives (Langergraber, Mitani & Vigilant, 2007). For example, a recent study by Koyama et al (2006) found that chimpanzees exchanged grooming and subsequent support in agonistic encounters. This exchange was partner specific, had a temporal component, and effectively ruled out symmetry based factors such as relatedness and association (e.g. "symmetry based reciprocity," de Waal & Luttrell, 1988). Similarly, some researchers report chimpanzees exchanging meat, fruit and other commodities for mating opportunities (Hockings et al, 2007; Gomes & Boesch, 2009; Stanford, Wallis, Mpongo, & Goodall, 1994; but see Mitani & Watts, 2001; Gilby, 2006 for reviews of the evidence opposing this "meat-for-sex" hypothesis). Chimpanzees also reciprocally groom each other over the long term (periods of seven to 12 months later); although it is unclear if close association other than kinship may have influenced these results (Gomes, Mundry, & Boesch, 2008).

These results have been confirmed in laboratory studies. In one experiment, if chimpanzee A groomed individual B in the morning, B was more likely to share food with A in the afternoon (de Waal, 1997a). This mental scorekeeping of favors given and received is called calculated reciprocity, and considered the most cognitively demanding

mechanism of reciprocal altruism (Brosnan & de Waal, 2002). Thus far, the evidence for calculated reciprocity is largely observational (but see below), and limited to chimpanzees.

Learned Reciprocity

Instead of assuming that individuals are born with calculated reciprocity, it is more likely that, like all complex social skills, learning plays a prominent role (de Waal & Suchak, in press). Individuals can learn that their partner's behavior is contingent upon their past behavior and then change their own behavior to manipulate their partner's future behavior.

Surprisingly few studies have actually examined whether or not individuals can learn these contingencies. In a recent study, a pair of orangutans developed reciprocity in a token transfer task (Dufour, Pelé, Neumann, Thierry, & Call, 2009). Each individual had access to a set of tokens that were only of value to their partner. One individual initiated the transfers and then over time, both partners began to alternate token transfers, thus learning to reciprocate with their partners. In contrast, chimpanzees failed to develop contingent reciprocity in a pulling task in which one individual could favor its partner, and vice versa (Brosnan et al, 2009). Individuals were no more likely to make decisions that benefited their partner if their partner had helped them in the past, than if their partner had behaved selfishly. Given that chimpanzees, are capable of calculated reciprocity in several different contexts as discussed above it is surprising that they did not develop reciprocity in this study. However, this study used a paradigm that had failed to produce prosocial behavior in the past. There is obviously little to learn about the

contingencies of prosocial behavior, if the behavior itself does not take place. Learned reciprocity requires a situation in which at least a minimal amount of help is spontaneously provided by individuals (de Waal, 2008).

Although the only studies of learned reciprocity thus far examined apes, monkeys are also quite good at learning contingencies. Specifically, since capuchins are highly tolerant, share food (de Waal, 1997b, 2000), and are known for cooperation in captivity (Mendres & de Waal, 2000) and in wild hunting situations (Perry & Rose, 1994), they are ideal subjects for studies on cooperation and reciprocity. This study will test capuchin monkeys to see if they can learn the contingencies between their own and their partner's behavior, and use this knowledge to develop a reciprocal exchange of favors. In doing so, we will test one of the main tenets of the strong reciprocity literature, which is that only humans cooperate with strangers. We will test capuchin monkeys with in-group and out-group members to explore the differences, taking into consideration that any exchange of favors with in-group members may have repercussions in daily group life whereas experiments with out-group members preclude any long-term consequences.

Inequity Aversion

Inequity aversion (IA) is a negative reaction to an unequal distribution of rewards (Fehr & Schmidt, 1999). In the study mentioned above, when the prosocial option was manipulated such that actors received an apple piece (consistent with the rest of the experiment) but the partner received a grape (a much better reward), prosocial token choice dropped to chance level, regardless of the relationship between the partners (de Waal et al., 2008). This increase in selfishness is an example of inequity aversion. These

results are consistent with previous studies that have demonstrated IA in capuchin monkeys (Brosnan & de Waal, 2003; van Wolkenten, Brosnan, & de Waal, 2007). Despite ongoing debate on this topic (Dubreuil, Gentile, & Visalberghi, 2006; Fontenot, Watson, Roberts, & Miller, 2007; Roma, Silberberg, Ruggerio, & Suomi, 2006), recent studies confirm the initial claim that IA requires a) a task (i.e. it does not work the same if food rewards are handed out for free), and b) a long string of trials to allow subjects to learn the contingencies. If these two conditions are met, IA has been confirmed for monkeys as well as dogs (Fletcher, 2008; Neiworth, Johnson, Whillock, Greenberg & Brown, 2009; Massen, van den Berg., Spruijt, & Sterck, under review; Range et al., 2009)

Clearly, IA of this type has the potential to impede cooperation and promote selfish behavior. Many studies have tested to see if monkeys exhibit inequity aversion and several have examined the factors that influence inequity aversion (Brosnan, Freeman & de Waal, 2006; Brosnan et al., in press). However, little attention has been given to whether or not individuals can develop a mechanism by which to overcome inequity aversion. Learned reciprocity might be one such mechanism; if individuals learn to reciprocate when the reward distribution is unequal, they can actually maximize the number of higher rewards they receive.

Cooperation with Unrelated Individuals

Cooperation biased towards kin has been extensively demonstrated in the literature across a wide variety of primates (reviewed by Gouzoules & Gouzoules, 1987). Unlike the claims of some strong reciprocity theorists (e.g. Boyd et al., 2003), examples

of cooperation with non-relatives are just as prevalent (Dugatkin, 1997; Langergraber et al., 2007). Specifically, several studies have demonstrated that capuchins readily cooperate towards a common goal and provide benefits to non-relatives in a variety of experimental contexts (Brosnan et al., 2006; de Waal, 2000; de Waal & Berger, 2000, de Waal et al., 2008; Lakshminarayanan & Santos, 2008). For example, a recent study by de Waal and colleagues (2008) showed that, when given the choice between a prosocial option that rewarded themselves and a partner and a selfish option that only rewarded themselves, capuchin monkeys picked the prosocial option more often than expected by chance when paired with unrelated group members. However, when paired with out-group "strangers," they were no more prosocial than expected by chance.

In general, there have been relatively few studies examining cooperation with strangers in capuchin monkeys and primates in general. Indeed, since there is little evidence in the field that cooperation between strangers occurs, why would primates have this capacity? Given that capuchins cooperate with non-relatives, however, perhaps under the right circumstances these tendencies could be extended to strangers in the same way that it has been argued that human cooperation with strangers may be an extension of a social psychology that evolved in the in-group context (Burnham & Johnson, 2005). Perhaps if individuals have the ability to learn about the advantages of cooperating with strangers, cooperation will emerge.

Learned Reciprocity in a Prosocial Choice Task: The Current Study

To summarize the above: capuchin monkeys have a well-developed tendency, which is influenced by both social closeness and reward distribution (de Waal, et al.,

2008; Lakshminarayanan & Santos, 2008). Whether or not individuals can use contingent reciprocity to exploit this tendency for mutually beneficial relationships based on reciprocity remains to be examined. In other words, monkey A may be able to learn that if it is prosocial and benefits B, then B may be prosocial in return, thus benefiting A. This could work to the advantage of B as well. Whether or not an individual is prosocial or selfish could be contingent on whether or not that recipient has helped them in the past. The present study aims to explore if capuchin monkeys can learn such a contingency associated with partner behavior. Specifically, the question being asked is whether capuchins will make prosocial or selfish choices based on a contingency with the choice their partner has made previously.

This study will use the token exchange paradigm of previous studies in which most of the time one partner made the token choices which then impacted both individuals in a pair (e.g. Brosnan & de Waal, 2003; de Waal et al., 2008). Whether or not capuchins can learn a contingency will be tested by moving from this one-subject paradigm to one in which both individuals alternate making choices (see Methods below). Alternating sessions will always be compared with sessions in which only one member of the pair is allowed to choose. Additionally, there are two other conditions to be compared: (1) prosocial behavior when there is an equal reward distribution versus when the reward distribution is unequal; and (2) prosocial behavior between non-kin, familiar pairs and unfamiliar pairs (with one monkey from each group; Table 1).

	Equal Rewards	Unequal Rewards
Single Actor Sessions	Prosocial Familiar>Unfamiliar	Chance level Familiar>Unfamiliar
Alternating Sessions	Prosocial Familiar=Unfamiliar	More Prosocial Familiar=Unfamiliar

Table 1. Summary of tests conducted and hypotheses.

Hypotheses

Hypothesis 1 – Alternating promotes prosociality. When given the chance to alternate making choices, capuchins will make a higher percent of prosocial choices than when only a single monkey is choosing. This would maximize the number of rewards each individual receives. The null hypothesis would be that there is no difference in the percent of prosocial choices across conditions.

Hypothesis 2 – Alternating leads to contingent reciprocity. If the monkeys increasingly pick the prosocial token when alternating it may be because they have developed a contingency between their choices and their partner's choices. In other words, if an individual learns that when she picks the prosocial token (which rewards both herself and her partner), her partner is more likely to pick the prosocial token in the next trial (thus giving her another reward), she should increasingly pick the prosocial token.

The null hypothesis would be that there is no contingency between an individual's choices and their partner's previous choices. If there is an increase in prosocial behavior,

but no contingency develops, the alternative hypothesis is that individuals are employing attitudinal reciprocity (de Waal, 2000).

Hypothesis 3 – Alternating compensates for IA. This study will also test to see if monkeys will be able to overcome inequity aversion by alternating in the manner described above. de Waal and others (2008) demonstrated that IA caused prosocial preferences to drop to chance levels (i.e. if the actor chose the prosocial token, both individuals were rewarded, but the partner received a better reward than the actor). Although IA should reduce the number of prosocial choices in the when only monkey is choosing, when given the chance to alternate, subjects should pick the prosocial token more than any other condition. During alternating sessions, picking the prosocial token reciprocally maximizes the number of desirable rewards they receive.

Hypothesis 3 – Individuals can learn to cooperate with out-group partners. As mentioned above, this study will compare token choices of non-kin, in-group pairs with unfamiliar, out-group pairs. When a single actor is choosing for an entire session, in-group pairs should pick the prosocial token more than out-group pairs. de Waal et al. (2008) demonstrated that monkeys picked the prosocial token at a higher level with increasing social closeness. However, when given the chance to alternate, both familiar and unfamiliar pairs should pick the prosocial token at the same rate if reciprocity develops.

These hypotheses are largely based on the idea that monkeys should be able to learn a contingency between their choices and a partner's choices (de Waal & Suchak, in press). One major alternative hypothesis is that instead of learning a contingency based

on their partner's behavior, they are associating the prosocial token with a greater number of rewards than the selfish token. In other words, they may learn that the prosocial token signifies that they always get a reward (regardless of whether they themselves or their partner chose it) whereas they only sometimes get a reward from the selfish token (if they chose it themselves). This would lead to the development of a preference for the prosocial token by the end of the experiment, and a complete disregard to partner choice (or even presence).

A second alternative hypothesis is that instead of learning a contingency based on their partner's behavior, they are learning a contingency based on the reward their partner's choice behavior has conferred upon them. In other words, they may learn that if they pick the prosocial token in the current trial they are more likely to get a reward in the next trial.

Methods

Subjects and Housing

Subjects were 12 brown capuchin monkeys (*Cebus apella*) housed in two separate social groups at the Yerkes National Primate Research Center. One group consists of 15 monkeys housed in 25 m^2, and the other of 11 monkeys in 31 m^2. The enclosures for both groups have indoor and outdoor areas. The two groups are visually, but not acoustically isolated from each other. The monkeys receive Purina monkey chow and water *ad libitum*, and trays containing fresh produce every evening. Monkeys were never food or water deprived.

The subjects for this test were 8 adult females (over the age of 6) and 4 juvenile males (between the ages of 4 and 6). Subjects were tested in pairs and each subject was paired with both a non-kin, familiar group member, and an unfamiliar partner from the other group (see Appendix A for a summary of subjects tested).

Six of the subjects tested in this experiment had extensive exchange experience. They had previously participated in three or four token exchange studies (e.g. Brosnan & de Waal, 2003; Brosnan & de Waal, 2004; van Wolkenten et al., 2007, and/or de Waal et al., 2008) and had been exchanging for six to ten years prior to the commencement of this study. These subjects were considered "experienced" at exchange tasks. The other six subjects tested were all new to the exchange paradigm and were considered "novices." All novices were extensively trained on the token exchange procedure similar to the training procedures the others received 10 years ago (Brosnan & de Waal, 2004). Novices also received training on associating tokens with different values (see Appendix B for training procedures). As experience with token exchange might affect behavior in this task, this factor was examined during data analysis.

Test Procedure

Subjects were separated from the group using an established separation procedure and placed in a familiar test chamber. For all test sessions the test chamber was divided into two equally sized (78 x 58 x 64 cm) compartments by a transparent lexan partition. Thus the partners could both see and hear each other, but had no physical contact and were unable to transfer food or other objects between them. The front of the test chamber was a transparent lexan panel with arm holes such that objects and food could be

exchanged between the experimenter and the monkeys. Each test session lasted approximately 20 minutes, at which point subjects were returned to their groups. All procedures were approved by the Institutional Animal Care and Use Committee (IACUC) prior to the commencement of the study.

Token Exchange

Tokens. This experiment utilized the token exchange paradigm of de Waal et al. (2008). Tokens for this study were 3.5 cm x 5 cm PVC pipes similar to those used in the previous study. Each condition utilized two different types of token, which were physically identical, but painted with visually distinct colors and patterns (Figure 1a). Because some subjects participated in the previous experiment, care was taken so that none of the tokens resembled those used previously. Six tokens (three of each type) were presented in a 13 cm x 23 cm shallow plastic bin (Figure 1b). In between every trial the experimenter "jumbled" the tokens by mixing them with her hand with her eyes closed. This jumble was intended to minimize any location biases for the monkeys and also any potential experimenter biases to lean the tray to one side or another.

(a)  (b) 

Figure 1 (a). Examples of two tokens. **(b).** The "jumble" of tokens.

Tokens carried different meanings as in de Waal et al. (2008). One token was designated as the selfish token. This token conferred an apple reward upon the actor only. The other token, the prosocial token, rewarded the actor with an apple and the partner with an apple or a grape (depending on the particular reward condition, see below). Thus, the actor always received an apple reward, regardless of which token was chosen. All rewards were approximately 1 cm^3 in size. Each reward condition utilized differently painted tokens and the values of the tokens were counterbalanced across pairs. For example, if for pair 1 the blue striped token was selfish and the orange spotted token was prosocial, for pair 2 the orange spotted token was selfish and the blue striped token was prosocial.

Exchange procedure. Each trial consisted of the experimenter presenting the actor (the monkey making the choice for that particular trial) with the jumble tokens in a dish, by holding it up to a predetermined location in front of the test chamber (approx. 5 cm from the bottom and 20 cm from the center of the test chamber, Figure 2a). The actor was given 30 seconds to select a token. Once the actor selected a token and took it into the test chamber, the experimenter held her hand in a begging gesture in front of the same hole the actor took the token through (Figure 2b). The actor had 30 seconds to return the token to the experimenter by placing it in her hand. The experimenter then placed the token in a clearly visible spot between both monkeys to remind them of the choice (Figure 2c). Within 5 seconds rewards were distributed to either or both monkeys according to the token choice (Figure 2d). Prior to delivering the rewards, the experimenter held up both rewards so that both monkeys could see their own and their

partner's rewards. After a 15 second inter-trial interval the next trial began. If the actor failed to choose or return the token within the allotted time, or the actor did not place the token in the experimenters hand (i.e. threw it on the floor or at the experimenter), the trial was cancelled, no reward given, and the inter-trial interval commenced. Each test session consisted of 30 trials.

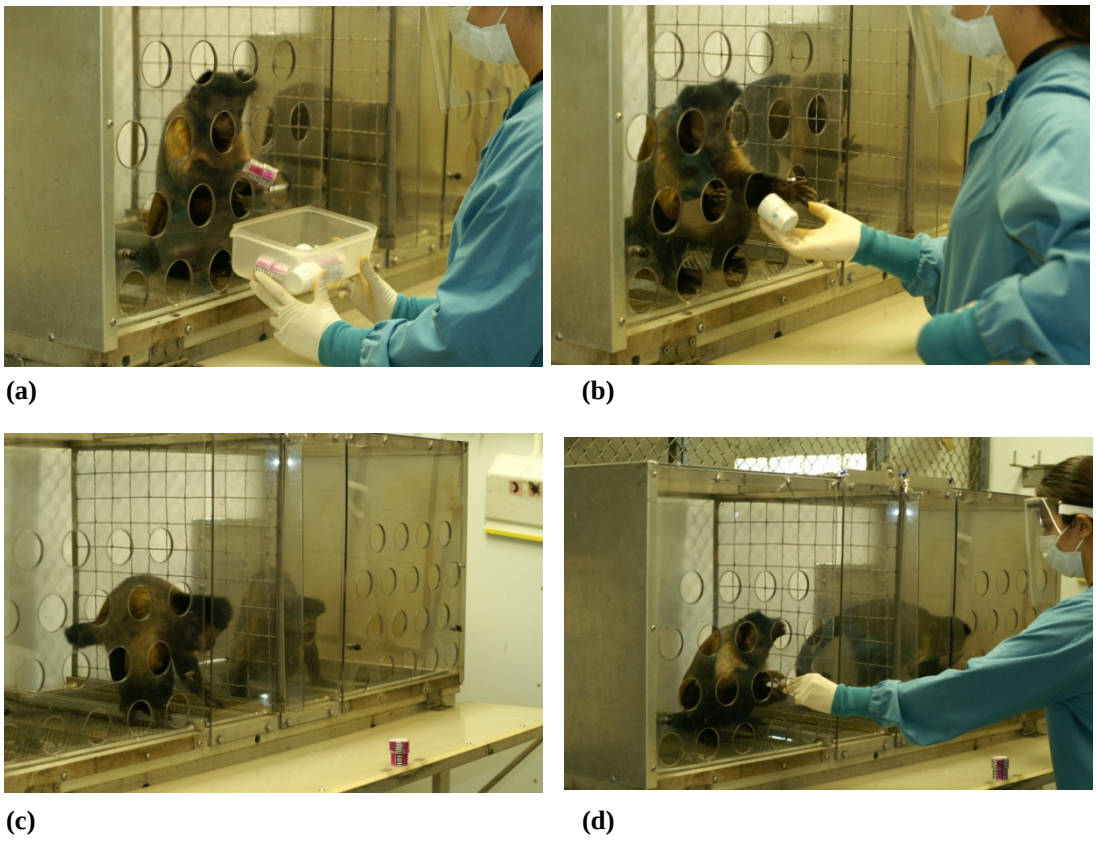

Figure 2. The token exchange procedure. **(a)** The actor choosing a token. **(b)** The actor returning the token. **(c)** The placement of the token prior to reward delivery. **(d)** Distribution of rewards.

Phase 1—Token Preference Tests. Token preferences were tested prior to the commencement of the study to make sure subjects did not have an inherent preference for either token. First, each subject was given 10 randomly ordered forced choice trials (where only one token type was present) to equate each token with a single piece of

cereal. Then each subject was given 20 free choices. If two or more subjects picked a token 80% of the time, or the average preference across subjects for any token was greater than 60%, both tokens were discarded, new ones painted and a new preference test conducted.

Phase 2—Familiarization. The purpose of this session was to familiarize the actor with the token values. This session consisted of 30 forced choice trials: 15 in which only the selfish token was available, 15 in which only the prosocial token was available. The order of the trials was randomly determined using an online random number generator (www.random.org). Exchanges were be rewarded differently by token, as described above.

Phase 3—Single Actor. Single Actor sessions were designed to test the level of prosociality individuals demonstrated without reciprocity involved. Procedure for these sessions was similar to that of de Waal et al (2008). One individual served as an actor for the entire session, the other as a passive partner. The actor was given 30 free-choice trials following the token exchange procedure described above. Prior to the commencement of this test, 6 forced-choice reminder trials (3 selfish and 3 prosocial) were given to help reinforce the values of the tokens. All Single Actor sessions were repeated on a second day to ensure that any learning effects had attenuated prior to moving on.

Phase 4—Alternating. Alternating sessions consisted of 30 trials as described above. These sessions differed from Single Actor sessions in that from trial to trial the role of actor and partner switched between both subjects. In other words, the monkeys alternated choosing tokens. As individuals should had already learned the token values by this session, there were no reminder trials at the beginning of the session. Alternating sessions were repeated for a second day to allow the monkeys to learn about their partner's behavior.

Phase 5—Control Conditions.

A. Control 1, Yoked Control. This control was designed to test the alternative hypothesis that monkeys were learning a contingency based on the rewards they received rather than their partner's choices. During this condition, only one individual was the actor, but the reward distribution mimicked the partner's choices from an Alternating session (see Table 2 for an example reward distribution from a Yoked Control session). Thus the partner's choices were "yoked" to choices they made during a previous session. Each individual had one Yoked Control session, following the Alternating sessions. If subjects were monitoring and responding to their partner's choices, their level of prosociality during the Yoked Control session should resemble that of Single Actor sessions. If they were responding to the rewards during the Alternating sessions, they should be more prosocial during the Yoked Control session than during the Single Actor sessions.

Example from unequal, Alternating session				Corresponding Yoked Control session			
Trial	**Individual exchanging**	**Token Choice**	**Reward for individual 1**	**Trial**	**Individual Exchanging**	**Token Choice**	**Reward for individual 1**
1	1	A	Apple	**1**	1	A or B	Apple
2	2	A	No reward	**2**	No exchange	----	No Reward
3	1	B	Apple	**3**	1	A or B	Apple
4	2	B	Grape	**4**	No exchange	----	Grape
5	1	B	Apple	**5**	1	A or B	Apple
6	2	A	No reward	**6**	No exchange	----	No Reward

Table 2. A comparison of an Alternating session and its corresponding Yoked Control session. The only difference between the two sessions is that during Alternating trials individual 2 was exchanging, but during the Yoked Control trials individual 2 did not exchange. The rewards distributed on those trials corresponded to the choices individual 2 made during the Alternating session.

B. Control 2—Partner Absent Tests. This control was designed to assess the subjects understanding of the tokens at the end of each reward condition and to rule out the possibility that individuals have simply developed a large preference for the prosocial token. Monkeys completed two test sessions without their partners. Procedures followed those of the Single Actor sessions except that there was no partner present. The order of the tests was counterbalanced across individuals.

Test 1—Open Panel. The lexan panel that divided the test chamber was open halfway allowing individuals to run around and take both rewards when they chose the prosocial token.

Test 2—Closed Panel. The lexan panel was closed. When the prosocial token was chosen, the second reward was held up to the empty side of the

test chamber for three seconds, but the individual could not access the reward.

See Appendix C for a list of test sessions.

Reward Conditions

Two different reward conditions were designed to test whether capuchins exhibited inequity aversion in this exchange task, and whether they could overcome inequity aversion through reciprocity.

Equal rewards. In this condition, the choosing the selfish token gave the actor an apple reward and the partner no reward. The prosocial token gave the actor an apple reward and the partner an apple reward.

Unequal rewards. In this condition, choosing the selfish token gave the actor an apple reward and the partner no reward. The prosocial token gave the actor an apple reward and the partner a grape reward. All subjects were tested to ensure they preferred a grape reward over an apple reward.

All 12 test days (see Appendix C) were conducted with each of these reward conditions for each pair. In between reward conditions each pair was given a one month break before moving to the next reward condition. During this break, subjects participated in a different exchange task where they were paired with a different partner. The purpose of this task was to ensure that there were no carry-over effects between conditions. Additionally, half of the pairs began with the equal reward condition and completed the unequal reward condition second; the other half had the opposite sequence. The monkey that served as individual 1 during the equal reward condition served as individual 2 during unequal rewards and vice versa.

Behavioral Data

Token choice was recorded live during all test sessions on a checklist and later confirmed from video. All sessions were recorded using a Canon DV recorder. Since a previous study (de Waal et al., 2008) indicated that the monkeys show behavioral differences depending on which token is chosen, several behaviors were also recorded (see Appendix D: Ethogram). Specifically, behavior was recorded during the eating phase, the period of time after the rewards were delivered and before the next trial began. Behavioral data may help confirm whether the subjects understand the meaning of the tokens. A subset of the test sessions were independently scored by another rater to test for inter-rater reliability.

Data Analysis

All statistical tests were run using Statistical Package for the Social Sciences (SPSS) version 17.0. For all tests alpha was set at .05. Prior to running all parametric statistical tests, all data were tested for normality using a 1-sample Kolmogorv-Smirnov test. For all significant tests, effect sizes were reported using η_p^2 for all ANOVAs and Cohen's d for all paired samples t-tests. All t-tests were two-tailed unless otherwise specified. For all tests alpha was set at .05 unless otherwise specified. If paired comparisons were run, a Bonferroni correction was used to control for experimentwise error.

Preference tests. Token preferences were tested prior to the commencement of testing. As pre-established criteria were used to evaluate preferences, no inferential

statistics were needed. Food preference tests were also conducted to ensure that when given a choice between a grape reward and an apple reward, individuals preferred the grape reward more than expected by chance. This was tested using a one-sample t- test.

Single Actor tests. As in de Waal et al (2008) test sessions were divided up into three ten-trial blocks to assess for learning. Trial blocks were compared using paired-samples t-tests. The two Single Actor sessions that each individual completed for each condition were compared using paired-samples t-tests. All of these analyses tested for learning effects within and between sessions.

Single Actor vs. Alternating sessions. Overall levels of prosociality were assessed using a 2 x 2 x 2 repeated measures factorial ANOVA. This tested for a main effect of reciprocity (Single Actor vs. Alternating), reward condition (equal vs. unequal), and partner (in-group vs. out-group), as well as any interactions between these variables. To control for the number of choices an individual was making, a second 2 x 2 x 2 repeated measures factorial ANOVA was run, comparing their first 15 choices in the single actor sessions to their first 15 choices in the alternating sessions.

Contingency testing. Whether or not the capuchins developed contingencies between their own and their partner's behavior during Alternating sessions was tested in two ways. First, logistic regression identified the degree to which an individual's choice was predicted by the partner's previous choice, previous two choices, and previous three choices. Second, the rate at which individuals chose the selfish or prosocial token following a prosocial or selfish choice by their partner was calculated. These rates were then compared in a 2 x 2 contingency table.

Controls. Yoked Control sessions were compared to the corresponding alternating session using a 2 x 2 x 2 repeated measures factorial ANOVA. Partner Absent Tests were analyzed in two ways. First, subjects' understanding of the token values was assessed by directly comparing their behavior during the Open- and Closed-Panel tests. These tests were compared using paired-samples t-tests. To test whether or not individuals developed a preference for the prosocial token, the amount they chose the prosocial token during the Closed-Panel test was also compared to chance using a one-sample t-test.

Behavioral Data. Behavioral data was calculated as a rate at which the behavior occurred during a particular choice (selfish or prosocial). These rates were then compared using a 2 x 2 repeated measures factorial ANOVA with the dependent variables of choice (selfish vs. prosocial), and type of session (Single actor vs. Alternating). Inter-rater reliability was tested using Cohen's kappa for all behavioral measures.

Results

I. Preference Tests

Token preference tests. All sets of tokens were tested to ensure that there were no inherent preferences prior to familiarization. Two criteria were set: (1) that across all individuals tested no token was preferred more than 60% of the time and (2) that no more than one individual preferred a given token 80% or more of the time. All tokens met both criteria. In fact, the highest preferred token was chosen an average of 53.13 ± 4.58 %, and no token was ever chosen more than 80% of the time by any monkey. Therefore, all tokens passed the preference test and no tokens had to be discarded.

Food Preference Test. All 12 individuals preferred grape over apple, choosing grape an average of 91.25 ± 12.99% of the time. This was significantly higher than chance ($t_{11} = 11.00$, $P < 0.001$).

II. Single Actor vs. Alternating Sessions

A. Single Actor sessions. The data were divided into three 10-trial blocks per session, for a total of six trial blocks (Figure 3). Subjects paired with in-group partners showed a significant increase in the percent of prosocial choices across the first session from the first trial block (trials 1-10) to the third trial block (trials 21-30; equal rewards: $t_{11} = 3.37$, $P = 0.003$, one-tailed; unequal: $t_{11} = 2.006$, $P = 0.035$, one-tailed). Although the percent of prosocial choices by out-group partners also increased over the course of the first session, this difference was not significant (equal: $t_{11} = 0.23$, NS; unequal: $t_{11} = 0.462$, NS). During the second Single Actor session, there is no significant change in the percent of prosocial choices across the trial blocks for any reward/partner conditions (in-group/equal: $F_{2,22} = 0.106$, NS; in-group/unequal: $F_{2,22} = 0.868$, NS; out-group/equal: $F_{2,22} = 0.949$, NS; out-group/unequal $F_{2,22} = 0.221$, NS). There were also no significant differences between the two Single Actor sessions for any reward/partner conditions ($F_{1,11} = .131$, NS). Therefore, the data from both sessions were combined for analysis. These results suggest that while learning may have taken place during the first session (particularly for the in-group pairs), subjects had learned the values of the tokens prior to moving on to the Alternating sessions. Additionally, there were no significant differences between experienced and novice subjects for any of the reward/partner conditions (in-group/equal: $t = 0.176$, NS; in-group/unequal: $t = -1.160$, NS; out-

group/equal: t = -0.956, NS; out-group/unequal: t = -1.630, NS; $\alpha = 0.0125$ (Bonferroni Correction)).

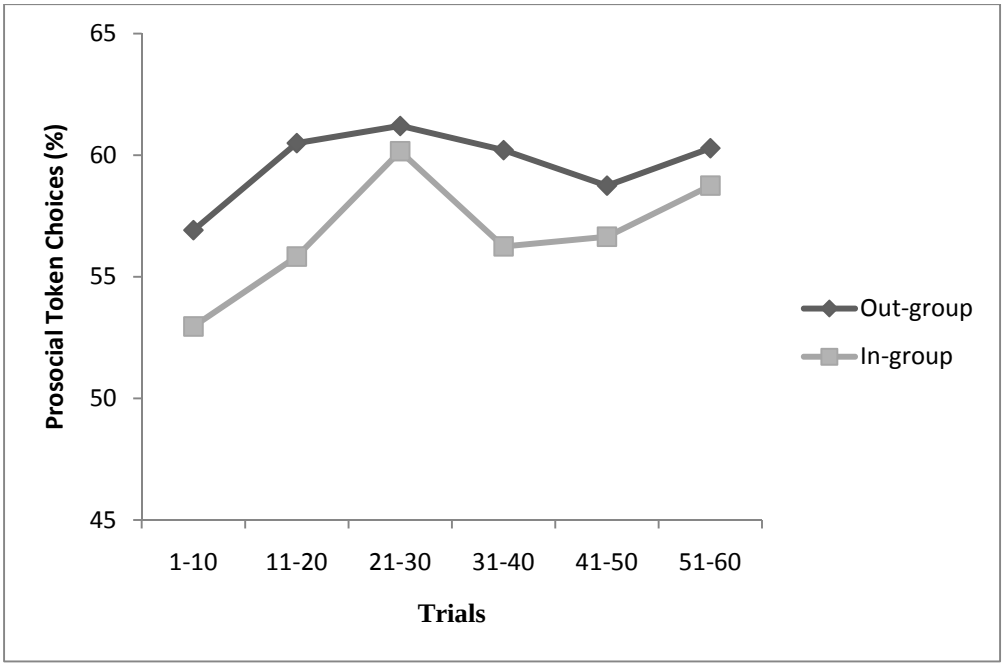

Figure 3. Percent of prosocial choices by trial block. The mean percent of prosocial choices for each 10-trial block. Since there were two single actor sessions, trials 1-30 are from the first session and 31-60 are from the second. In-group pairs chose the prosocial token at a significantly higher rate during the third trial block (trials 21-30) as compared to the first trial block (trials 1-10). Otherwise there were no significant differences within or between sessions (e.g. comparing trials 1-30 to trials 31-60)

B. Alternating sessions. There were no significant differences in the percent of prosocial choices when each session was divided into three 10-trial blocks for any reward/partner conditions (in-group/equal: $F_{5,55} = 1.29$, NS; in-group/unequal: $F_{5,55} = 1.19$, NS; out-group/equal: $F_{5,55} = 2.21$, NS; out-group/unequal: $F_{5,55} = 0.55$, NS). There were also no significant differences between the two Alternating sessions for any reward/partner conditions ($F_{1,11} = 1.84$, NS). Therefore, the data from both sessions were combined for analysis.

The level of prosocial behavior increased from the Single Actor sessions to the Alternating sessions with a moderate effect size ($F_{1,11} = 26.11$, $P < 0.001$, $\eta_p^2 = 0.70$). When the analysis was restricted to only the first 15 choices by each individual (for each condition), there was an even stronger effect ($F_{1,11} = 37.88$, $P < 0.001$, $\eta_p^2 = 0.78$).

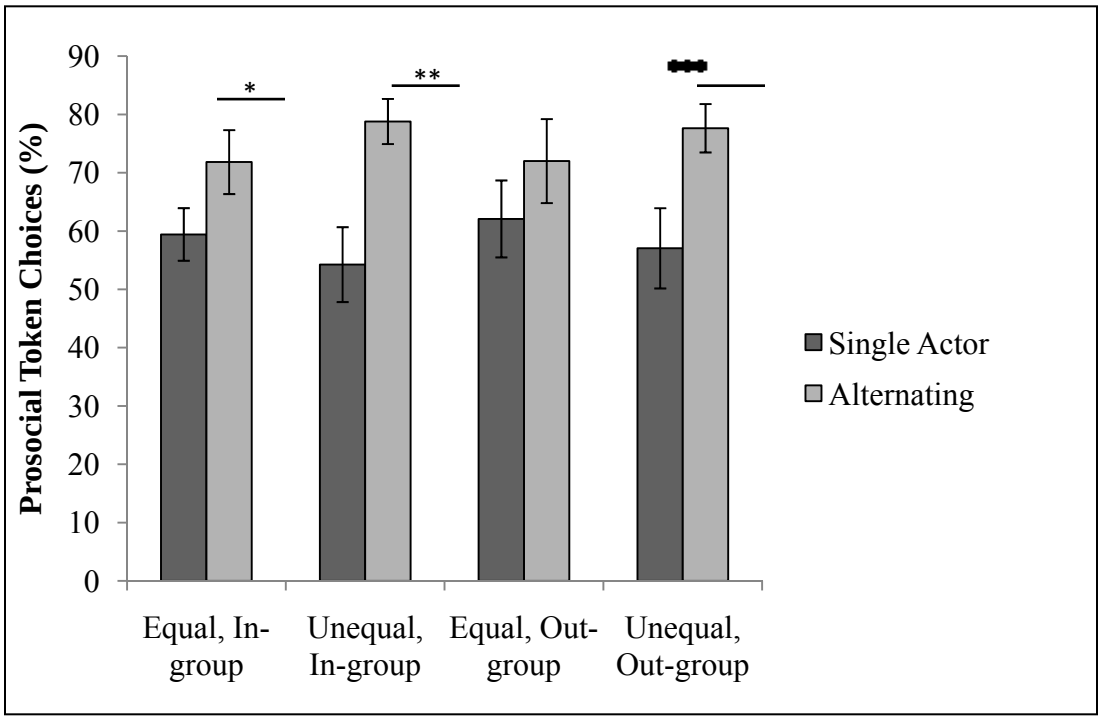

Figure 4. Comparison of Single Actor and Alternating Sessions for each partner/reward condition. The mean (± SEM) percent prosocial choices during Single Actor and Alternating sessions. There were more prosocial choices in Alternating sessions than Single Actor sessions for in-group partners regardless of reward distribution and out-group partners with unequal rewards. * denotes $P < .05$, ** denotes $P < .01$, *** denotes $P < 0.001$.

One further follow-up analysis was run comparing single actor and alternating sessions for all four reward/partner conditions for each individual. Nine out of twelve individuals chose the prosocial token significantly more during Alternating sessions than during Single Actor sessions (Table 3). Of the three individuals that did not show a significant increase, Star and Gretel showed the opposite effect in the equal/in-group sessions. In other words, both individuals picked the prosocial token less during Alternating sessions as compared to Single Actor sessions when paired with in-group

partners with equal rewards. Similarly, Nancy decreased from Single Actor to Alternating during out-group/equal rewards sessions.

Individual	Single Actor (M ± SD)	Alternating (M ± SD)	Z-score
Star	45.88 ± 10.53	66.75 ± 10.43	1.46
Bias	65.38 ± 23.77	82.50 ± 13.39	1.83*
Nancy	41.88 ± 10.66	50.38 ± 27.27	0.92
Winnie	58.38 ± 26.95	74.35 ± 17.45	1.83*
Bailey	69.63 ± 33.39	91.63 ± 16.75	1.83*
Lulu	60.13 ± 15.22	75.88 ± 9.36	1.83*
Wilma	49.38 ± 12.76	66.88 ± 8.77	1.83*
Gretel	57.50 ± 9.12	69.88 ± 24.25	1.10
Snarf	67.63 ± 29.93	92.38 ± 11.09	1.83*
Luther	58.38 ± 24.77	76.13 ± 9.58	1.83*
Wookie	52.5 ± 12.02	70.88 ± 3.01	1.83*
Benny	81.00 ± 17.98	92.50 ± 12.77	1.83*

Table 3. A comparison of Single Actor and Alternating Sessions by individual. A z-score of 1.83 indicates that in all four partner/reward conditions the individual chose the prosocial token more in alternating sessions than in single actor sessions. * denotes $p<.05$, all P-values were one-tailed for this analysis.

C. Contingency between choices in Alternating sessions. Logistic regression tested whether or not an individual's choice in trial *n* could be predicted by their partner's previous choice, two choices, or three choices. There was no significant effect of the partner's previous choice or choices on the actor's choice for any of the partner/reward

conditions. Follow-up analysis compared the rates at which individuals chose a prosocial or selfish choice following a particular choice by their partner. Overall no significant contingency could be demonstrated; individuals picked the prosocial token at the same rate regardless of whether or not their partner had previously picked a prosocial token (χ^2 = 0.000, NS; Table 4).

		Partner's Choice at trial *n-1*	
		Selfish	Prosocial
Actors Choice	Selfish	81	219
at trial *n*	Prosocial	288	779

Table 4. A 2 x 2 contingency table illustrating the number of choices made by all individuals across all alternating sessions as a function of their partner's choice in the previous trial.

D. Behavioral Data.

1. Trials. Behavioral data was collected from all Single Actor and Alternating sessions, for a total of 4290 trials. Failures to exchange were rare: there were 61 trials in which there was no choice (1.42 %) and 46 trials in which the actor failed to return the token (1.08%). Since all failures to exchange resulted in cancellation of the trial and no rewards were given, these trials were not scored for behavior. Therefore, a total of 4183 trials were scored.

2. Inter-rater reliability. A randomly chosen subset of test sessions was scored by another rater. Since the inter-rater reliability on face and body orientation was quite poor (Kappa = 0.45) these measures were excluded from the analysis. Inter-rater reliability for affiliative behavior, measured as mutual positive interest, was extremely

high during the Single Actor sessions(Kappa = 0.95), however, when Alternating sessions were included, agreement dropped considerably (although still considered acceptable, Kappa = 0.60). Agonistic behavior was extremely rare, occurring on only 2% of trials (100 out of 4183 trials). As it was extremely rare, it was impossible to establish inter-rater reliability. Furthermore, 93% of occurrences of agonistic behavior occurred when one of two individuals (Star or Winnie) were in the testing chamber, regardless of condition or test session. Therefore, agonistic behavior was not used in the final analysis.

3. Affiliative behavior. Affiliative behavior was measured as mutual positive interest between the two partners, which occurred in 375 of the 4183 trials analyzed (9%). Overall, pairs had significantly more mutual positive interest after the prosocial token had been chosen than when the selfish token had been chosen, with a small effect size ($F_{1,11} = 9.09$, $P = 0.012$, $\eta_p^2 = 0.45$). Interestingly, the overall rate of mutual positive interest significantly decreased from Single Actor sessions to Alternating sessions, also with a small effect size ($F_{1,11} = 6.94$, $P = 0.027$, $\eta_p^2 = 0.37$), although there was still more mutual positive interest associated with prosocial choices than selfish choices (Figure 5).

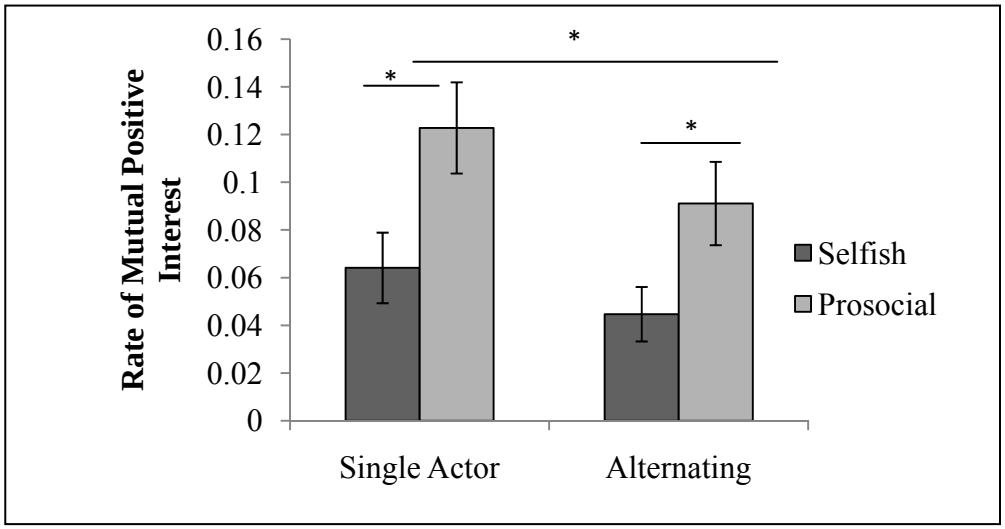

Figure 5. Affiliative Behavior by Session. The mean (± SEM) rate of mutual positive interest during Single Actor and Alternating Sessions. Individuals exhibited a higher rate of mutual positive interest following prosocial choices than following selfish choices. The overall rate of mutual positive interest significantly decreased from Single Actor to Alternating sessions as well. * denotes $P < 0.05$.

III. Equal vs. Unequal Rewards

In both Single Actor and Alternating sessions, the percentage of prosocial choices during equal reward conditions did not significantly differ from the percentage of prosocial choices during unequal reward conditions; there was no main effect of reward condition on prosocial choices ($F_{1,11} = 0.034$, NS). There was, however, a significant interaction between reward condition and alternating, with a small effect size ($F_{1,11} = 5.20$, $P = 0.043$, $\eta_p^2 = 0.32$). During Single Actor sessions individuals chose the prosocial token at a higher rate when rewards were equal than when rewards were unequal; the opposite was true for Alternating sessions (Figure 6). When the analysis was restricted to only the first 15 choices each subject made for each condition, the effect was even stronger ($F_{1,11} = 9.13$, $P = 0.012$, $\eta_p^2 = 0.45$).

Although the percent of prosocial choices were not significantly different from equal sessions to unequal sessions, follow-up analyses were conducted comparing the

rate of prosocial token choice to chance. During the Single Actor sessions the prosocial token was chosen at a higher rate than expected by chance when rewards were equal (in-group: $t_{11} = 1.832$, P = 0.047; out-group: $t_{11} = 2.086$, P = 0.031) but not when rewards were unequal (in-group: $t_{11} = 0.662$, NS; out-group: $t_{11} = 1.023$, NS, Figure 7).

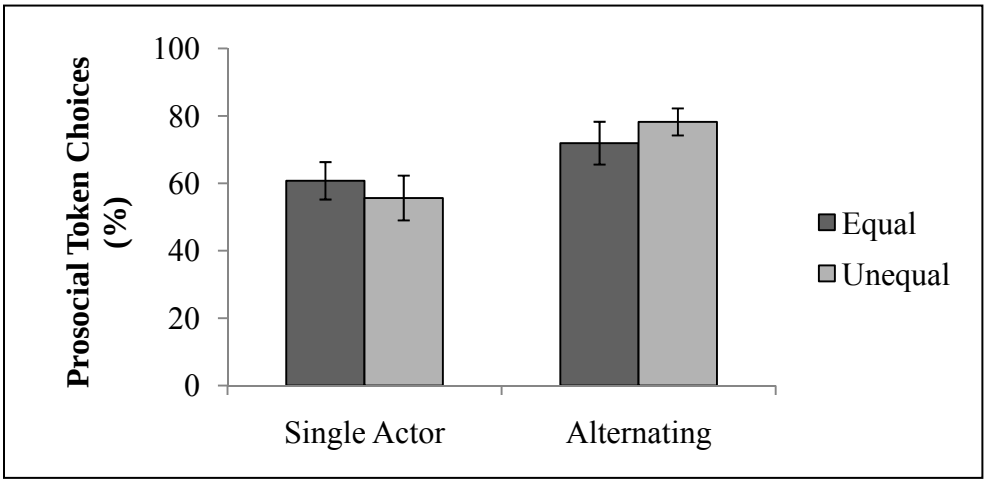

Figure 6. A Comparison of Equal and Unequal Rewards. The mean (± SEM) percent prosocial choices during each reward condition. There is a significant interaction between reward and session type: individuals pick the prosocial token more during equal rewards than unequal reward during the Single Actor sessions, but during alternating sessions the opposite is true.

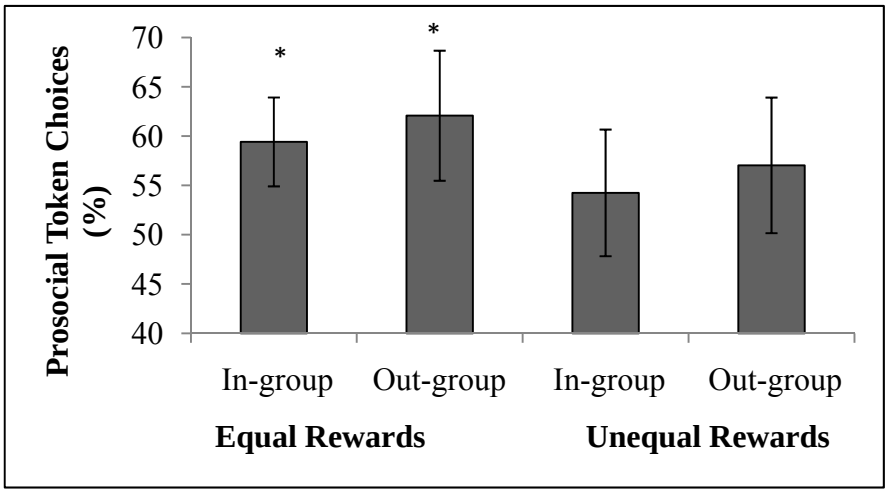

Figure7. Percent of Prosocial Choices by Reward Condition Compared to Chance. The mean (±SEM) percent prosocial choices during each reward/partner condition. During Single Actor sessions with equal reward conditions, the percent of prosocial choices was significantly higher than chance (50%, dashed line). However, when the reward distribution was unequal, individual's picked the prosocial token at chance levels.
* denotes significance at the .05 level.

IV. In-group vs. Out-group Partners

There was no significant difference between in-group and out-group pairs across conditions ($F_{1,11} = 0.067$, NS Figure 8). There was no interaction between pairing and Single Actor/Alternating sessions ($F_{1,11} = 0.422$, NS) or between pairing and reward condition ($F_{1,11} = 0.004$). Even when the young males were removed from the analysis, there was still no significant difference between in-group and out-group partners ($F_{1,7} = .029$, NS).

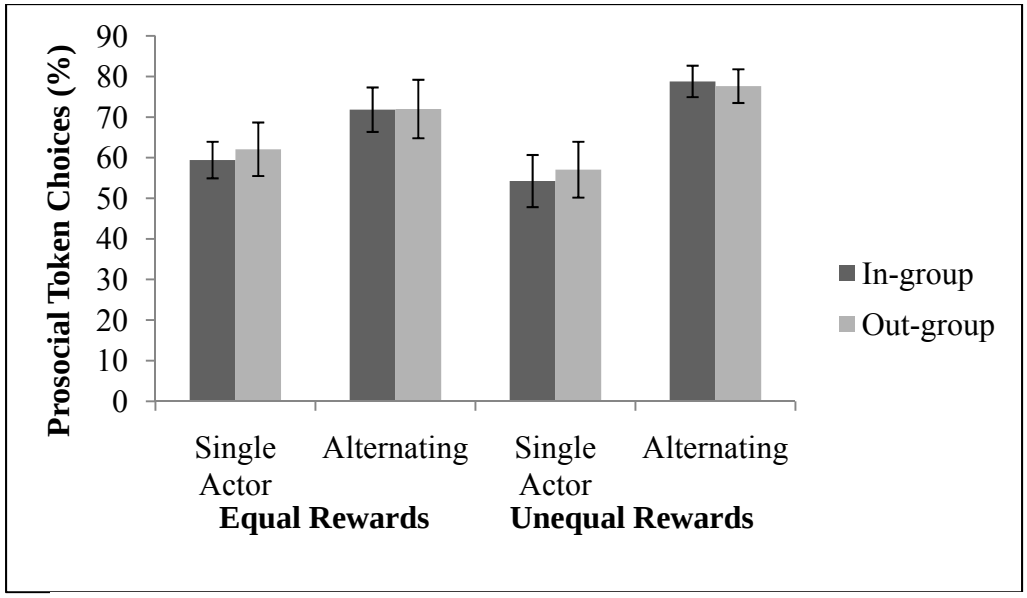

Figure 8. Comparison of in-group and out-group pairs across sessions. The mean (± SEM) percent of prosocial choices by subjects paired with in-group and out-group partners. There were no significant differences between in-group and out-group pairs across any of the test sessions.

V. Controls

A. Yoked Control. There was a main effect of condition, such that individuals picked the prosocial token less during the Yoked Control Test than during it's corresponding alternating session ($F_{1,11} = 11.99$, $P = 0.005$, $\eta_p^2 = .522$; Figure 9). There was no significant main effect of pairing (in-group/out-group: $F_{1,11} = 0.001$, NS) or reward condition (equal/unequal: $F_{1,11} = 1.71$, NS). There were also no significant

interactions (Pairing X Reward: $F_{1,11} = 0.002$, NS; Pairing x Condition: $F_{1,11} = 0.912$, NS; Reward x Condition: $F_{1,11} = 0.051$, NS; Pairing x Reward x Condition: $F_{1,11} = 1.266$, NS).

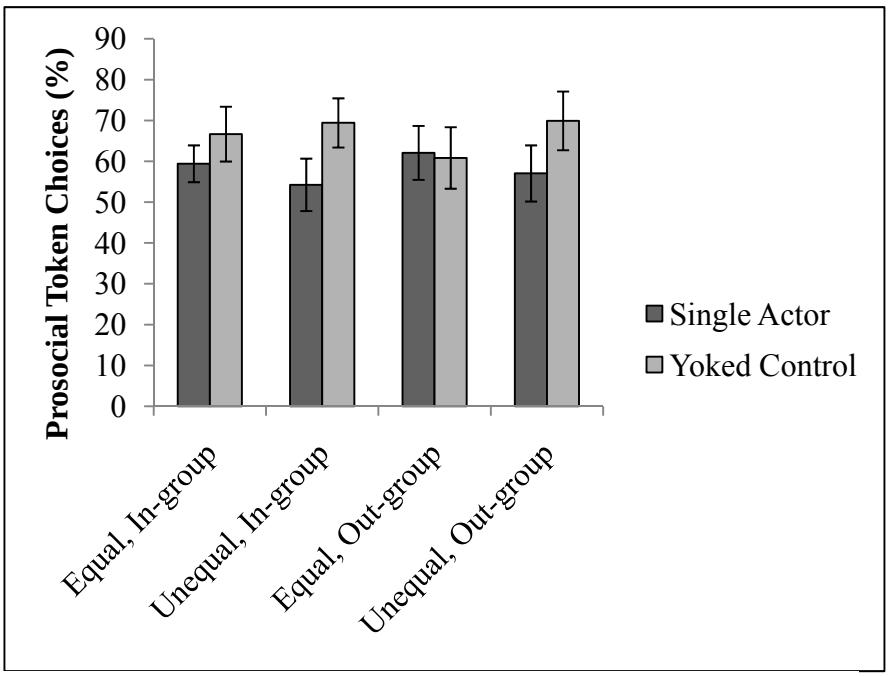

Figure 9. Comparison of Single Actor and Yoked Control Sessions. Mean (± SEM) percent of prosocial choices during the Single Actor and Yoked Control sessions. For equal rewards, pairs had no significant difference in the percent of prosocial choices between the Single Actor and Yoked Control session. However, when rewards were unequal, there was a significant increase in the percent of prosocial choices from the Single Actor to the Yoked Control sessions.

B. Partner-Absent Tests. For all reward/partner conditions, individuals chose the prosocial token significantly more during the open-panel test than during the closed-panel test (in-group/equal: $t_{11} = 7.53$, $P < 0.001$, $d = 2.87$; in-group/unequal: $t_{11} = 4.28$, $P = 0.001$, $d = 1.91$; out-group/equal: $t_{11} = 5.44$, $P < 0.001$, $d = 1.68$; out-group/unequal: $t_{11} = 4.72$, $P = 0.001$, $d = 2.10$; $\alpha = 0.0125$ (Bonferonni correction); Figure 11), suggesting that they understood the values of the tokens. Furthermore, none of the closed panel tests were significantly different from chance, suggesting that they had not developed a

preference for one token over the other (in-group/equal: t_{11} = -0.34, NS; in-group/unequal: t_{11} = 1.71, NS; out-group/equal: t_{11} = -0.01, NS; out-group/unequal: t_{11} = 2.09, NS; α= 0.0125 (Bonferonni correction)).

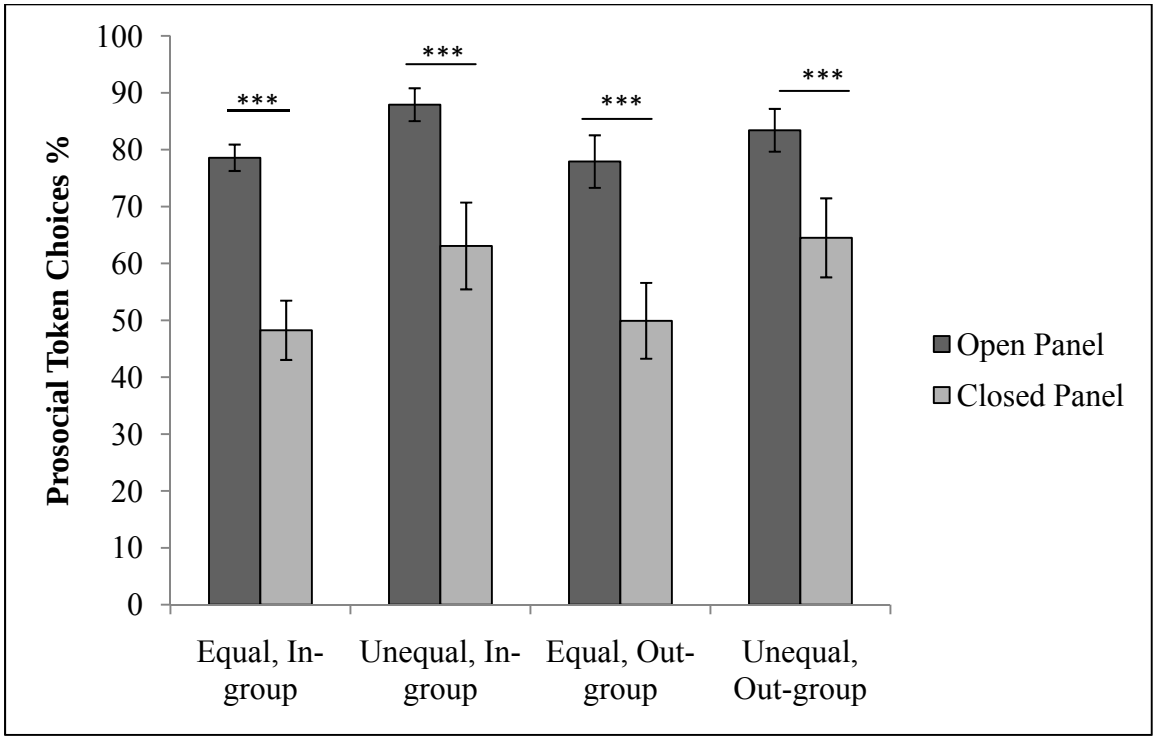

Figure 10. Partner Absent Tests. Mean (± SEM) percent prosocial choices during the two types of partner-absent tests. Individuals picked the prosocial token significantly more during open panel test than closed panel tests, suggesting they understood the values of the tokens. *** denotes P < 0.001.

Discussion

Learned Reciprocity or Mutualism?

Results of the experiment support the hypothesis that prosocial behavior would increase when individuals alternated making choices. However, monkeys in this task failed to develop a contingency between their own and their partner's behavior. Specifically, they were equally likely to choose the prosocial token regardless of whether

their partner had previously made a prosocial or selfish choice. It is possible that instead of contingent reciprocity, the monkeys were demonstrating attitudinal reciprocity, which goes by the catch-phrase "if you're nice, I'll be nice" (de Waal, 2000). This could explain the increase in prosocial behavior without a contingency. Instead of keeping precise tit-for-tat track of their partner's previous choices, the alternation between them and frequent prosocial choices increased a mutual positive attitude. Because of the short time intervals and non-reliance on scorekeeping, attitudinal reciprocity is close to mutualism.

Potentially, the increase in prosocial choices from single actor to alternating sessions could be ascribed to the development of a preference for the prosocial token. This hypothesis is countered by the outcome of our control tests, however. The Partner-Absent tests confirm that although the monkeys understood the meanings of the two tokens, they had no preference for the prosocial token, because they only picked the prosocial token at chance levels during the closed panel tests. Another argument against the alternative hypothesis of a developed preference is that the monkeys exhibited an increase in prosociality only during sessions in which their partner was actually making choices, not during the Yoked Control.

Although these results seem consistent with previous research that chimpanzees also do not develop a contingency in a prosocial decision-making task (Brosnan, et al., 2009), they are probably result from a completely different mechanism. It seems unlikely that the chimpanzees in that experiment were also exhibiting attitudinal reciprocity instead of contingent reciprocity, as their overall level of prosocial behavior was no different from chance throughout the sessions. However, both studies illustrate that in quickly repeated interactions, these primates do not seem to be learn a contingency

between their own and their partner's behavior. For chimpanzees, this lack of contingent reciprocity seems to lead to a breakdown in cooperation, but capuchins may have developed a simpler alternative that promotes cooperation equally as well.

The results of this study are actually quite similar to those reported in orangutans (Dufour et al., 2009). In that study orangutans developed an exchange of favors, which led to an increase in cooperation across the test sessions, without the formation of a contingency. The orangutans pattern of behavior could easily be explained by attitudinal reciprocity. One individual was cooperating and the other simply mirrored their behavior. Similarly, in the current study, there was an increase in prosocial behavior across sessions without development of a contingency.

In general, the reward structure may be responsible for the prosocial tendencies these monkeys exhibit both when acting alone and during reciprocal interactions with a partner. When the prosocial token is chose, individuals are able to eat together. Previous studies have demonstrated social facilitation of eating in our capuchin monkeys (Dindo & de Waal, 2006). It is possible that the desire to eat together is a proximate mechanism mediating prosocial behavior in capuchins. However, other primates, such as common marmosets, will altruistically donate food to a partner while receiving nothing themselves (Burkart et al., 2007). The prosocial tendencies demonstrated in this task cannot be explained by the desire to eat together because the actor does not have access to food.

Inequity Aversion

The results of this experiment support the hypothesis that individuals will exhibit Inequity Aversion (IA) during the single actor task, but will overcome that reaction when

given the opportunity to alternate. Even though the difference between equal and unequal single actor sessions was non-significant, the results are in the same direction as the previous study (de Waal et al., 2008) in that prosocial behavior during unequal rewards dropped to chance level. When subjects alternated making choices, they chose the prosocial token more frequently, collectively maximizing the number of valuable rewards they received.

The results for the unequal reward conditions must be interpreted cautiously, however. During unequal rewards, the prosocial token conferred an apple reward on the actor and a grape reward on the partner. Subjects may have been so motivated to get a grape, that they may have stopped paying attention to the fact that their partner was *choosing* to give them a grape. Instead, they may have associated the prosocial token with the possibility of getting a grape (even though when they chose it themselves, they only got an apple). Although the results of the Partner Absent Tests confirmed that individuals understood the values of the tokens and had not developed a preference for the prosocial token, the results from the Yoked Control demonstrate that individuals were responding to the rewards obtained rather than their partner's choice. Future studies could compare lower foods of unequal values (for example, a cucumber and an apple) to see if individuals can overcome inequity aversion while still paying attention to their partner's choices.

Cooperation with Strangers

The results of this study failed to support the hypothesis that there would be an interaction between the social closeness of the partner and the level of prosociality or

tendency to exchange benefits in alternating sessions. We found no significant difference in behavior towards in-group and out-group partners for any type of reward condition. In fact, throughout the sessions out-group partners chose the prosocial token at a slightly higher rate than in-group partners. While it was expected that there would be no difference during the alternating sessions, the findings for the single actor sessions are particularly surprising. The previous study demonstrated that subjects picked the prosocial token above chance with both kin and non-kin, familiar partners, but that with out-group partners they dropped to chance level (de Waal et al., 2008).

Several factors may have contributed to the difference between the current study and that of de Waal et al. (2008). First, there was considerable variability in the familiarity of out-group partners with each other. Out of six out-group pairs, two had tested together regularly before (including in the previous token exchange study), two had had just one test session together (using the barpull apparatus in an unrelated task), and two had had no experience together at all. Although a follow-up analysis did not reveal a significant difference between pairs that had tested together before and those that had not, the number of pairs that we could compare was obviously very small. A more systematic study specifically examining this effect is perhaps necessary. For example, an individual's behavior with an out-group partner they have tested with previously could be compared with their behavior with a complete stranger. Furthermore, subjects that were common to both token exchange studies (and had the same partners for both studies) could specifically be examined to see if they had any change in behavior between the two studies.

Second, unlike the previous study, which tested only adult females with extensive task experience (de Waal et al., 2008), the present study also used young males. These males were all at the age where they would leave their natal group under natural conditions. In the closely related white-faced capuchin (*Cebus capucinus*), young males have been observed interacting affiliatively with out-group males in the wild (Jack & Fedigan, 2004). On some occasions, these interactions actually resulted in the males transferring groups. Perhaps it is beneficial at this age to be friendly with other young males, even strangers. It is impossible from the current study to draw any distinctions between male and female behavior with out-group partners as there were only four males; and age and sex were confounded (all the males were juveniles, all the females adults). In general, the juvenile males were more prosocial with out-group partners than adult females, although this difference cannot be evaluated statistically with the current subject pool.

This study clearly demonstrates that capuchins will readily cooperate with familiar non-relatives from their own group, but also with out-group members. Under the right artificial conditions, these monkeys have the capacity for prosocial behavior and learned reciprocity with outsiders, a characteristic which the strong-reciprocity literature often depicts as uniquely human.

Conclusion

Although this study was not directly testing whether monkeys were strong reciprocators per se, we examined some of the elements that may contribute to strong reciprocity in human society. In capuchin monkeys, there was no evidence of the

element of punishment that is characteristic of strong reciprocators. Following a selfish choice, an individual with a predisposition to punish should withhold a reward from their partner by selecting the selfish token. This was not observed in the present study in which capuchins chose the prosocial token at the same rate regardless of their partner's previous choice.

The second characteristic of strong reciprocators is prosocial behavior, even towards strangers. In the current study, capuchins achieved extremely high levels of prosocial behavior (nearly 80% of the time during alternating sessions) likely as a result of attitudinal reciprocity. Furthermore, across all sessions, prosocial tendencies were just as strong between stranger monkeys as between familiar partners. By the definition of the strong reciprocity literature, monkeys in this experiment were not "true" strangers, which can only be achieved in one-shot interactions (Fehr, Fischbacher & Gachter, 2002). However, this study demonstrates that capuchin monkeys have a latent capacity to cooperate with individuals outside their social group, which is not something they (or most other nonhuman primates) ever do in the wild. It seems unlikely that their cooperative tendency with strangers evolved independently from within-group cooperation, as it is more likely an extension of same tendency. This has been suggested to be the case also for human cooperation with strangers (Akçay et al., 2009; Burnham & Johnson, 2005), even though the strong reciprocity literature postulates a separate evolutionary path for cooperation with strangers (Fehr & Fischbacher, 2003; Boyd et al., 2003). Our data thus seem to support the former school of thought.

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Appendix A. Summary of Subjects Tested

Name	Sex	Age	Years of exchange	Number of exchange studies	Familiar partner	Unfamiliar partner
Star	F	39	10	4	Bias	Nancy
Bias	F	20	10	4	Star	Winnie
Nancy	F	24	10	4	Winnie	Star
Winnie	F	25	10	4	Nancy	Bias
Gretel	F	6	0	0	Bailey	Wilma
Wilma	F	12	6	3	Lulu	Gretel
Bailey	F	10	0	0	Gretel	Lulu
Lulu	F	24	10	4	Wilma	Bailey
Snarf	M	6	0	0	Benny	Luther
Benny	M	6	0	0	Snarf	Wookie
Luther	M	4	0	0	Wookie	Snarf
Wookie	M	5	0	0	Luther	Benny

Appendix B: Training Procedures

Novice subjects completed four stages of training, outlined below. Each stage utilized different tokens and was more complex than the previous stage. In order to move on to the next stage of training, subjects had to meet a criterion of 85% correct exchanges. During stage 1, this was exchanging the token using the proper procedure for 85% of trials. For stages 2-4, criterion was picking the high-value token 85% of the time. If an individual did not meet criterion for a particular stage, that test was repeated (utilizing different tokens) until they passed.

Stage 1—Learning the token exchange procedure. Subjects were trained to exchange the token using procedures similar to that of Brosnan and de Waal (2004). First, subjects were given 30 trials to see if they would spontaneously exchange a blank, white token. For the two subjects who failed to exchange within those 30 trials (Benny and Gretel), the procedure was shaped. Although most subjects spontaneously exchanged, all required training on the exact exchange procedure used in this experiment (see Methods). All trials for stage 1 in which individuals exchanged correctly were rewarded with one piece of Kix cereal. Once subjects exchanged using the proper procedure during 85% of the trials, they moved on to Stage 2.

Stage 2—Associating two tokens with differently valued rewards. After subjects learned how to properly exchange, they were trained to associate visually distinct tokens with different valued rewards. Choosing the high-value token resulted in a banana reward, the low-value, a celery reward.

A. 90 familiarization trials- Subjects were given 90 forced choice trials (3 sessions) to learn the values of the tokens. The order of the trials was determined using a random number generator (random.org). Following their familiarization trials, subjects were tested to see if they preferred the high-value token. Subjects had to choose the high-value token 85% of the time to move on to Stage 2B.

B. 30 familiarization trials- Subjects established that they could associate differently colored tokens with different rewards, but they had to demonstrate this ability with fewer forced-choice trials. Subjects were trained using the same procedures above, except with only 30 forced-choice trials (1 test session) to learn the token values.

Stage 3—Associating two sets of tokens with differently valued rewards. After subjects learned to associate visually distinct tokens with different valued rewards, they had to learn the values of 6 tokens, 3 of each high- and low-value rewards. This was to mimic the "jumble" of tokens used in the experiment.

A. 90 Familiarization trials- Same as stage 2A, except with 6 tokens instead of 2.

B. 30 familiarization trials- Same as stage 2B, except with 6 tokens, instead of 2.

Stage 4—Associating two sets of tokens with different numbers of rewards. The prosocial paradigm requires that individuals learn that the prosocial token delivers two rewards (one to each the actor and the partner) and the selfish token delivers one reward (to the actor only). Choosing the high-value token during stage 4, therefore, delivered

two Kix cereal rewards, one to each side of the test chamber. The lexan partition was open, allowing individuals to take both rewards. The low-value token delivered only one Kix cereal reward.

A. 90 familiarization trials—Same as 3A except with different token values.

B. 30 familiarization trials—Same as 3B except with different token values.

Once subjects successfully completed stage 4, they were eligible for participation in the experiment.

Appendix C. Order of Test Sessions Conducted for Each Reward Condition

Day	Session	Role of Individual 1	Role of Individual 2
1	Familiarization	Actor	Partner
2	Single Actor, day 1	Actor	Partner
3	Single Actor, day 2	Actor	Partner
4	Familiarization	Partner	Actor
5	Single Actor, day 1	Partner	Actor
6	Single Actor, day 2	Partner	Actor
7	Alternating, day 1	Actor 1	Actor 2
8	Alternating, day 2	Actor 2	Actor 1
9	Yoked Control	Actor	(Partner)
10	Yoked Control	(Partner)	Actor
11	Partner Absent Test 1	Open Panel	Closed Panel
12	Partner Absent Test 2	Closed Panel	Open Panel

Appendix D: Ethogram

Aggressive behaviors:

Scored as 1/0 (occurred/did not occur) for each trial:

TE	Threaten experimenter	Gives a threat face or threat bark directed to the experimenter
TP	Threaten Partner	Gives a threat face or bark to the partner

Distress behaviors:

PR	Protest	Gave a protest scream
FF	Fear Face	Made a fear face

Face Orientation:

1	Monkey is clearly facing partner, obviously looking directly at partner
2	Monkey is facing lateral to the partner
3	Monkey is facing away from the partner

Body Orientation

1	Monkey's body is positioned towards the partner's body.
2	Monkey's body is lateral to the partner's body.
3.	Monkey's body is pointed away from the partner's body.

Affiliative Behavior

Scored as 1/0 (occurred/did not occur) for each trial:

MPI	Mutual Positive Interest: Affiliative behavior characterized mutual orientation to each other, sitting close to the partition, and/or eyebrow flashing, presenting, or lip-smacking by both individuals.

Failures to complete an exchange:

NC	No token choice within 30 sec
NR	No return within 30 sec
FR	Subject fails to properly return the token (i.e. throws it at the experimenter, on the ground, etc.)