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Prosocial Motivations of Capuchin Monkeys

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Abstract

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Prosocial behaviors in humans are known to be motivated by empathy and intrinsic gratification known as "warm glow". Historically thought to be uniquely human, similar self-rewarding mechanisms were recently proposed to motivate other-regarding behavior in brown capuchin monkeys (*Cebus apella*). To determine if capuchins are indeed motivated to be prosocial by a sense of satisfaction derived from helping another individual (i.e. "warm glow") or instead by a desire to eat at the same time as another individual, twelve capuchin monkeys underwent two types of tests. The first ("Token Exchange") paired subjects with a partner and allowed them to choose to be prosocial (reward both monkeys) or selfish (reward only the choosing monkey). In the second ("NE Control"), the same monkeys were paired but the choice was eliminated; the experimenter simply delivered food rewards according to choices made during the "Token Exchange." The occurrence of mutually affiliative behaviors per subject during prosocial and selfish outcomes in both tests was recorded and compared. The rate of affiliative behavior was found to be higher during a prosocial than a selfish outcome in both the Token Exchange and NE Control, suggesting that affiliative behavior is facilitated by the presence of two food rewards and, thus, the opportunity to eat together. Therefore, capuchin monkeys may be motivated to be prosocial by a sense of satisfaction derived from eating

with another individual. Surprisingly, the overall rate of affiliative behavior was also found to be higher during the NE Control than during the Token Exchange, indicating that the circumstances under which food is being delivered and consumed may likewise affect affiliative behavior overall.

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Introduction

Humans have long been considered a prosocial species. Countless examples of people helping unrelated individuals are cited not only anecdotally but in scholarly literature as well, seeming to demonstrate that this behavior is a component of human nature (Fehr & Fischbacher, 2003). By definition, prosocial behavior occurs when individuals perform actions that are beneficial to others, sometimes at a cost to themselves (Twenge et al., 2007). Many helping behaviors can be classified as prosocial and are often divided into two categories: altruistic behaviors and other-regarding behaviors. Altruism is a type of prosocial behavior in which the performer incurs a cost by helping another individual (de Waal, 2008). Conversely, other-regarding behavior denotes instances in which individuals help others at no cost to themselves (Burkart et al., 2007). The existence of prosocial behavior to various degrees in humans is hardly to be argued against, but if we begin to consider the *reasons* behind its existence, suddenly the evidence is not so clear-cut.

When describing the origins of a behavior, causality can be explained in terms of the proximate and the ultimate. As explained by Mayr (1961), proximate causes are environmental and biological factors that cause responses at the individual level. Thus, the immediate mechanisms that motivate an individual to perform a behavior fall under proximate causation. Ultimate causes, on the other hand, govern the long-term effects of a behavior that then act as selective pressures to affect the evolutionary fitness of individuals who perform it, thereby determining whether the propensity to perform the behavior becomes inherited by subsequent generations and, eventually, prevalent enough to be deemed species-typical. In short, the reason the behavior evolved and therefore exists in the first place in a species describes its ultimate cause. While the present study is focused on the proximate causes of prosociality, it is important to note that in order for the origins of prosocial behavior to be fully understood, both the proximate and the ultimate causes should be considered.

On the ultimate level, the most prominent explanations for prosocial behavior involve reciprocal prosocial exchanges and kin selection (Hamilton, 1964; Trivers, 1971). A specific example of reciprocal exchanges of prosocial behavior in the literature is reciprocal altruism (Brosnan & de Waal, 2002). Reciprocal altruism occurs when one individual performs a costly prosocial act on behalf of another, who then reciprocates with a costly prosocial act on behalf of his benefactor in the future. Prosocial acts being reciprocally exchanged, however, do not necessarily have to be costly. Rather, the implication is that the prosocial act benefits the recipient immediately but does not benefit the performer unless the recipient reciprocates in the future. A core component of reciprocal exchange is that individuals who have previously received help are likely to return the favor if their benefactor needs help in the future (Fehr, 2004). This not only directly improves the fitness of the individual who initially offered assistance, but also builds a positive reputation for both individuals, subsequently increasing the chance of receiving help in the future. Important to note here is that the exchanges occur over time, unexpectedly enough or far enough in the future that the individuals are probably unaware of and therefore unmotivated by any potential return benefits (Brosnan & de Waal, 2002). Alternately, if individuals choose to improve the welfare of a relative, they indirectly improve their fitness by helping to ensure the survival of shared genes (Hamilton, 1964; Trivers, 1971). In fact, Form and Nosrow (1958) demonstrated that following a natural disaster, people will first help family members, then familiar but unrelated individuals, followed finally by strangers. In this way, reciprocal exchange and kin selection act as mechanisms by which prosocial behavior potentially results in direct or indirect fitness benefits for performers (Hamilton, 1964; Trivers, 1971).

Ultimate explanations aside, the present study is concerned with the proximate mechanisms for prosociality. Given the fact that prosocial behavior requires one individual to spontaneously consider the welfare of another, often on behalf of the potentially unrelated or even completely unfamiliar recipient, it seems reasonable to ask: why would an individual choose to be prosocial? The answer to this question, at least in mammals, may lie in empathy, a proximate basis for a prosocial impulse that allows us to respond spontaneously to the sight of another in need (de Waal, 2008). Thus, empathy may be an automatic response that in turn may affect prosocial motivations and allow us to spontaneously act prosocially without necessarily considering the behavior's implications for ourselves or consciously taking the perspective of the individual we are helping. After individuals act upon this prosocial impulse to improve the welfare of another, it is possible that they subsequently associate helping others with an intrinsic, emotional benefit (de Waal, 2008).

Thus, although the performer of a prosocial act may provide goods or services with or without incurring a cost and without immediately profiting in return, this does not necessarily equate to a lack of benefits. In fact, while the recipients are endowed with a tangible benefit, their benefactor might receive benefits in the form of good feelings (Crumpler & Grossman, 2008). Known as the "warm glow" effect, humans often report feelings of happiness and gratification after improving a fellow individual's welfare (Andreoni, 1989). Interestingly, these positive experiences and self-reported "good moods" subsequently cause individuals to engage more frequently in social interactions and act more prosocially (Cunningham, Steinberg, & Grev, 1980; Isen, 1970). Thus, it seems that "warm glow" is circular: helping another individual may increase positive feelings, and positive feelings in turn may increase the propensity to help another individual. In this way, "warm glow" may act as a proximate cause of prosociality, motivating an individual to act prosocially both as a direct result of and precursor to the prosocial behavior.

A large component of prosocial behavior, whether in the form of altruism or other-regarding preferences, is communication between the helping individual and the individual being helped (Cunningham, Steinberg, & Grev, 1980). For example, following a prosocial act, perceived satisfaction may be expressed by increased eye contact and decreased physical distance between humans (Argyle & Dean, 1965; Kleinke, 1986). Moreover, prosocial individuals tend to communicate empathy by maintaining eye contact, leaning forward, decreasing physical distance, and verbally expressing their feelings (Haase & Tepper, 1972). In this way, nonverbal and verbal cues from either the performer or recipient of a prosocial act can play a large role in reflecting an understanding of how welfare is being affected (Cunningham, Steinberg, & Grev, 1980).

Although prosociality has been studied extensively in humans, the presence of prosocial tendencies in other species was not acknowledged until relatively recently. Self-motivated cooperation in animal and insect species has been observed since Wilson (1975) established the field of sociobiology in the 1970s, but the existence of other-regarding, prosocial motivations were not accepted until much later. When studies began to extensively demonstrate prosociality in eusocial insects, kin selection could easily be pinpointed as the primary mechanism for the behavior's existence. Prosocial tendencies towards non-relatives have since been demonstrated outside of humans, but even so, the majority of these studies examine only whether the behavior is present and do not address the question of motivation. In order to gain more valuable insight into the proximate causes of prosociality in humans, studies need to be conducted that focus on the proximate causes of prosociality in other species.

Findings of prosocial behavior in nonhuman primates have been particularly informative. Common marmosets (*Callithrix jacchus*), for example, have been found to provide food to a partner even if they receive no food themselves rather than to provide food for neither themselves nor their partner (Burkart et al., 2007). Furthermore, in a study of our closest living relative, chimpanzees (*Pan troglodytes*) were shown to spontaneously help unrelated conspecifics gain access to a food reward (Warneken et al., 2007). Beyond the experimental setting, Frans de Waal (2007) describes numerous instances of chimpanzees helping one another. In one example, he tells the story of Peony, an aging and arthritic female who often receives help from younger chimps when she is having trouble climbing—a simple gesture with which we can identify, but the extent to which chimpanzees will go to help one another, often even risking their lives to save a conspecific's, is perhaps the most compelling evidence that humans are not the only species to put others' needs before their own.

Perhaps the largest setback to research regarding prosocial behavior in animals is that discussions of prosocial origins often fail to distinguish between ultimate and proximate causes. Animal behaviors such as food-sharing, grooming, consolation, and coalition-forming are disqualified from prosociality on the basis that they are guided by self-interest, namely in the form of the propensity for direct or indirect benefits (Warneken et al., 2007). But as de Waal (2008) explains, the common claim that animals behave solely according to self-interest assumes that they are capable of fully understanding how an outcome will benefit them. Those who reject prosociality in animals in this way are stating that prosociality is too complex a behavior for a nonhuman species to possess and then assigning complex cognitive abilities in order to explain why this is true. Aside from pointing out the limitations to an animal's ability to link the distantly future benefits of prosociality with the original act that may have produced them, de Waal (2008) asserts that this lacks evolutionary parsimony. In other words, the relationship between ultimate and proximate causes in nonhuman primates is no different than in humans: understanding the ultimate causes of prosociality says little about the actual motivations involved.

Thus, now that prosociality has been identified in primates, it is important to identify its proximate causes. Just as empathy has been found to motivate prosociality through an innate impulse in humans, it has been proposed that a similar empathic mechanism applies to primates. In support of this hypothesis, rhesus infants have been shown to respond to the cries of one another with embraces (de Waal, 1996, as cited in de Waal, 2008) and post-aggression consolation has been identified in chimpanzees (de Waal & van Roosmalen, 1979, as cited in de Waal, 2008). These findings provide evidence that empathy exists in primates and may therefore act as a proximate mechanism that leads to prosocial tendencies. While in humans this has been taken one step further to demonstrate that helping others is motivated by derived intrinsic benefits, or "warm glow," prosocial behavior in primates as facilitated by similar intrinsic benefits has been little studied. Thus, this study is concerned with identifying whether we share this proximate factor with other primates. Namely, we will identify whether "warm glow" exists as a motivation for prosocial behavior in the brown-tufted capuchin monkey (*Cebus apella*).

The existence of prosocial tendencies in capuchin monkeys has been demonstrated by de Waal, Leimgruber, and Greenberg (2008), who presented monkeys with the choice to be prosocial (providing a reward for themselves and a partner) or selfish (providing a reward only for themselves). Because bartering monkeys received the same reward regardless of choice, choosing to be prosocial incurred no direct cost and was thus a demonstration of "other-regarding," as opposed to altruistic, tendencies. This was important because it allowed for a clearer examination of whether monkeys took others' welfare into account: if all else was equal, did monkeys prefer outcomes that benefited others over those that did not? Remarkably, it was found that capuchin monkeys overwhelmingly chose to be prosocial. This indicated that some aspect of acting prosocially must have been intrinsically rewarding, motivating the capuchins to choose the prosocial option, but the basis for the intrinsic rewards could not be determined. Equally important were the observations that, when choosing whether to be prosocial or selfish, the monkeys' behavior suggested that both the monkeys making the decision (hereafter referred to as actors) and their partners had an understanding of the task and, additionally, were aware of the choices being made. Not unlike humans, the monkeys were more likely to orient towards one another and exchange affiliative signals following a prosocial decision. Conversely, a selfish decision was both preceded and followed by more back-turning and increased distance between the individuals.

Similarly, in a follow-up study that comprises the first part of the present two-part study, Suchak (2010) demonstrated that positive interactions (termed affiliative behavior and including known positive behaviors such as eyebrow-flashing and lip-smacking) occurred three times more often following a prosocial choice than following a selfish choice, suggesting that prosocial choices produced a positive emotional reaction more than selfish choices. Furthermore, the actor was significantly more likely to make a prosocial decision following an occurrence of affiliative behavior than following neutral behavior, indicating that, in the same way that positive mood motivates humans to help others, capuchins may have been motivated by affiliative interactions to act prosocially (Heyler, Suchak, & de Waal, 2009). These results likewise suggested that actors understood the consequences their choices had for their partner, that partners were aware when another monkey had an effect on their welfare, and that both communicated this understanding through behavioral cues (Suchak, 2010).

However, while the monkeys' overwhelming decision to be prosocial and the increase in affiliative behavior following a prosocial outcome both indicated that prosociality was rewarding, it could not be determined exactly why this was so (de Waal et al., 2008; Suchak, 2010). It is possible that the "warm glow" mechanism that motivates humans to behave prosocially similarly allows capuchins to derive a sense of satisfaction from the act of actually choosing to improve another's welfare. That capuchins chose to be prosocial following an affiliative interaction significantly more often than they chose to be selfish suggests that having a positive encounter with a conspecific motivates them to help in the same way that "warm glow" motivates humans (Heyler, Suchak, & de Waal, 2009). However, capuchins are known to be quite social when eating, sitting closely to and interacting with conspecifics during feeding periods (de Waal, Luttrell, & Canfield, 1993). Because food rewards are given to both individuals following a prosocial decision but only to the actor following a selfish decision, capuchins might simply enjoy eating together. Thus, it remains to be determined whether the capuchins were motivated to be prosocial because of a desire to help another individual or because they do not want to eat alone.

In the present study, we are concerned with addressing this question by examining whether affiliative behavior corresponds to particular choices or reward distributions. Our hypothesis and an alternative hypothesis are as follows:

1. Prosocial choice hypothesis: Affiliative behavior is facilitated by choosing to be prosocial. Therefore, capuchin monkeys may be

motivated to be prosocial by a sense of satisfaction derived from helping another an individual.

2. Social eating hypothesis: An alternative explanation is that affiliative behavior is facilitated by the presence of two food rewards and, thus, the opportunity to eat together. Therefore, capuchin monkeys may be motivated to be prosocial by a sense of satisfaction derived from eating with another individual.

This was tested by removing the decision-making process from the task used by Suchak (2010) and simply delivering rewards to both monkeys (mimicking the reward distribution of a prosocial choice) or reward to one monkey only (mimicking the reward distribution of a selfish choice). By comparing the rate of affiliative behavior following a prosocial outcome to the rate following a selfish outcome when decision-making is present and when decision-making is absent, we can determine if choosing to be prosocial is self-rewarding for capuchins or if eating together is motivating the behavior. There are two proposed outcomes:

1. If the ratio between rate of affiliative behavior following a prosocial outcome and that following a selfish outcome decreases when decision-making is removed, then the prosocial choice hypothesis is likely correct. In other words, if affiliative behavior is a response to prosocial choices, the monkeys will be equally affiliative during the selfish and prosocial outcomes and less affiliative overall when the rewards are delivered without a choice being made.

2. Alternately, if the ratio between rate of affiliative behavior following a prosocial outcome and that following a selfish outcome remains the same when decision-making is removed, then the social eating hypothesis is likely correct. In other words, if eating together is rewarding, there will still be significantly more affiliative behavior following a prosocial outcome than following a selfish outcome when the rewards are delivered without a choice being made.

Method

Subjects

Subjects were twelve capuchin monkeys (*Cebus apella*) housed in two visually separated social groups at the Yerkes National Primate Research Center in Atlanta, Georgia. These included 4 subadult (< 6 years old) males, 8 adult (> 6 years old) females. Subjects were tested in same-sex pairs and pairs were comprised of a subject with either a familiar, non-kin partner from the same group (hereafter in-group), or an unfamiliar partner from the other group (hereafter out-group). Every monkey had one in-group and one out-group partner and every pair remained consistent throughout. Testing did not interfere with the subjects' regular feeding schedule, which includes Purina monkey chow two times per day and fruit and vegetables once daily. Subjects were never deprived of food or water, which was available *ad libitum*.

During testing, the pair was temporarily removed from their respective groups and placed in a familiar test chamber that was visually and tactilely separate from the group. For all sessions, the test chamber was divided in two equally sized (36x60x60 cm) compartments by a transparent partition. Each monkey was placed in a separate compartment, with compartment side being assigned randomly in in-group pairs and assigned to be on the same side as the home group in out-group pairs. The partition, while preventing physical contact and food sharing between the subjects, allowed for social interaction through visual and vocal contact. Each session was separated into a series of trials that comprise of an individual acting as actor and directly interacting with the experimenter while the other individual acted as partner. Experimenters were able to interact with subjects in a controlled manner and with minimal distractions. Subjects did not participate in any more than one test for the study on any given day.

Procedure

This study involved a comparison between two different task types. The first type is termed "Token Exchange" and was run by Malini Suchak as part of the follow-up study mentioned previously (Suchak, 2010). The task used in this study is termed "No Exchange" (hereafter NE) Control. Data from the NE Control are being collected for this study, while data from the Token Exchange were collected for a previous study and are being used solely for comparison. All procedures were approved by the Institutional Animal Care and Use Committee (IACUC) of Emory University.

Token Exchange. The first experiment (conducted by Malini Suchak) utilized a token exchange task similar to that of de Waal et al. (2008). During each trial, the experimenter stood in front of the actor, who was then presented with six tokens divided into three each of two types: prosocial and selfish. All tokens were identical in size and shape, but prosocial and selfish were visually distinct in color and design (Figure 1). Choosing a prosocial token provided a food reward to both the actor and the partner, while choosing a selfish token provided a food reward to the actor only. Actors were familiarized with token values prior to testing. The six tokens (three of each type) were presented to the actor in a random jumble in order to prevent side bias. Actors had to select one token and then return it to the experimenter's outstretched hand (Figure 2, a-b). Trials in which an actor attempted to pick both tokens or did not pick a token within 30 sec were indicated as "No Choice" and discarded. Trials in which the actor chose a token but did not return it to the experimenter within 30 sec were indicated as "No Return" and discarded. The returned token was then placed upright in a visible but out of reach spot in front of both monkeys. The experimenter then delivered the rewards within 3 sec according to the actor's choice. Subjects had 15 sec to consume the reward. Thirty such trials composed one test session.

For each session, there were two possible reward distributions: equal rewards (both monkeys receive an apple) and unequal rewards (actor receives an apple and partner receives a grape, which is known to be a more desirable reward (de Waal, 1997). Thus, there were a total of four possible conditions: equal rewards with in-group partner; equal rewards with out-group partner; unequal rewards with in-group partner; and unequal rewards with out-group partner. Every subject was actor twice and partner twice in each of the four conditions, for a total of eight sessions per subject.

Figure 1. Examples of visually distinct tokens, one indicating a prosocial outcome and the other indicating a selfish outcome

Figure 2: The token exchange procedure. (a) token selection, (b) token return

No Exchange (NE) Control. The second experiment tested the exact same pairs, reward and partner conditions, and order of tests as the Suchak (2010) experiment, but the token task that served as the decision indicator was eliminated. Just as before, there were two possible reward distributions (equal and unequal) and two possible partners (in-group and out-group) for a total of four possible conditions: equal rewards with in-group partner; equal rewards with out-group partner; unequal rewards with in-group partner; and unequal rewards with out-group partner. However, every subject was actor only once and partner only once in each of the four conditions, for a total of four total sessions per subject, twelve total sessions per condition, and forty-eight total sessions overall. For each subject, one of the two data sheets for each condition was randomly selected and used to exactly recreate testing environment (e.g. on which side of the test chamber the subject was place) and reward distribution.

During each trial, the experimenter kept all interactions with subjects consistent with those during the Token Exchange (Suchak 2010), removing only the token exchanging component. In other words, the experimenter also stood in front of the actor in the exact same manner for 15 sec, but no tokens or tasks of any kind were presented. Any trials that had been indicated "No Choice" or "No Return" were skipped. The experimenter then delivered the rewards within 3 sec according to the exact sequence of the actor's choices recorded on the data sheet from the Token Exchange. Subjects then had 15 sec to consume rewards. In summary, in each trial, one reward was simply delivered to the actor or one reward each was delivered to both the actor and the partner based on previous decisions made by the actor in that pair for that particular condition. Thirty such trials composed one session.

Data coding

All test sessions were recorded on digital media. Behavior was coded according to an ethogram—a list of specific behaviors that were chosen and agreed upon by the experimenters prior to coding. This list was used to score for the frequency of behavior displayed during testing. The behavior recorded was the occurrence (indicated by a 1) or non-occurrence (indicated by a 0) of mutually affiliative behavior in a trial. Any trials indicated as “No Choice” or “No Return” were not coded. Affiliation was defined as any behavior that involved one or a combination of the following directed by each monkey at one another, regardless of location in the testing cage and lasting for at least 1 sec: staring at one another (provided there is no sign of aggression in the staring), lip-smacking (rapid opening and closing of the mouth), eyebrow-flashing (raising of the eyebrows), reaching fingers around partition towards one another, and placing hands up to partition. For our purposes, affiliation had to be expressed simultaneously by both monkeys for it to be recorded.

The same observer recorded all 48 sessions from the NE Control, as well as 19 (40 percent) of the 48 sessions from Suchak’s (2010) Token Exchange. Six of the 19 sessions (a total of 180 trials) from the Token Exchange were randomly selected and independently coded by Suchak for inter-rater reliability. Cohen’s kappa (κ) was calculated for agreement on the occurrence of affiliative behavior in the six sessions (180 trials) and was found to be $\kappa = 0.95$. Because this is considered high agreement, Suchak also coded the remaining 29 trials from the Token Exchange.

For both the Token Exchange and NE control, the rate of affiliative behavior per prosocial outcome for each actor was calculated by adding up the total number of prosocial-outcome trials in which affiliative behavior occurred for an actor and dividing by the total number of prosocial-outcome trials (excluding “No Choice” and “No Return”) for that actor. Likewise, the rate of affiliative behavior per selfish outcome for each actor was calculated by summing the total number of selfish-outcome trials in which affiliative behavior occurred for an actor and dividing by the total number of selfish-outcome trials (excluding "No Choice" and "No Return") for that actor. Overall rates of affiliative behavior for each actor were calculated by summing the total number of trials (selfish-outcome and prosocial-outcome) in which affiliative behavior occurred for an actor and dividing by the total number of trials (selfish-outcome and prosocial-outcome) for that actor.

Data analysis

The behavioral data collected was analyzed using a Repeated Measures Factorial ANOVA. For the ANOVA, there were 4 factors: 1) trial outcome (selfish or prosocial), 2) exchange condition (Token Exchange or NE Control), 3) reward condition (equal or unequal rewards), and 4) partner condition (in-group or out-group). Each subject's behavior was compared to itself within each of the two-part factors. Any significant effects in the Token Exchange were then compared to the significant effects during the NE Control.

Results

Rate of affiliative behavior was defined as the frequency of affiliative interactions per trial of a particular outcome. For each pair and each condition, the rate of affiliative behavior was subjected to a Repeated Measures Factorial ANOVA with 4 factors: 1) trial outcome (selfish or prosocial), 2) exchange condition (Token Exchange or NE Control), 3) reward condition (equal or unequal rewards), and 4) partner condition (in-group or out-group). A one-sample Kolmogorov-Smirnov test was used to test for normal distribution.

Although 2 of the 16 combinations of conditions produced significant results, ANOVA analyses of these two variables were interpreted cautiously.

There was a significant effect of trial outcome ($F_{1,11} = 16.16$, $p = 0.002$). Specifically, subjects exhibited affiliative behavior following a prosocial outcome about 1.5 times more often than following a selfish outcome during the NE Control (Fig. 3). This difference is consistent with that found in Suchak's (2010) Token Exchange, when subjects were about twice as likely to exhibit affiliative behavior following a prosocial outcome than following a selfish outcome (Fig. 4).

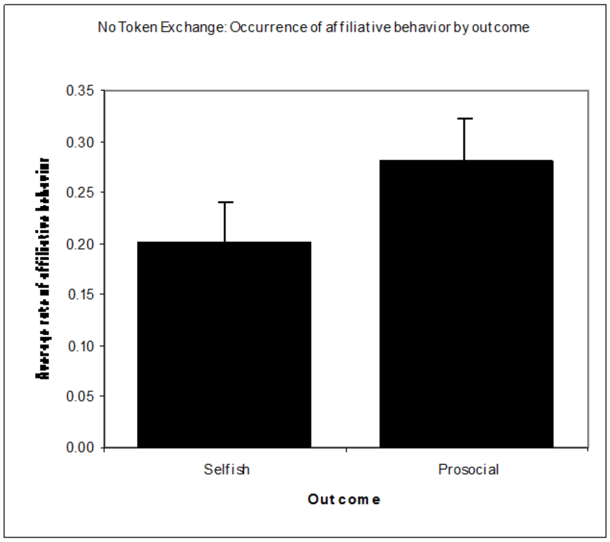

Figure 3. Rate of affiliative behavior following selfish (SEM = 0.04) and prosocial (SEM = 0.04) outcomes during the "no exchange" task. Subjects were significantly more affiliative following a prosocial outcome than following a selfish outcome.

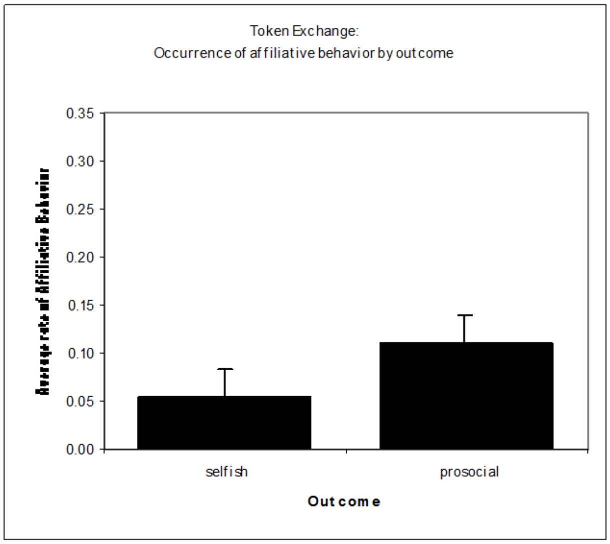

Figure 4. Rate of affiliative behavior following selfish (SEM = 0.01) and prosocial (SEM=0.02) outcomes during the token exchange task. Subjects were significantly more affiliative following a prosocial outcome than following a selfish outcome.

There was also a significant effect found of the exchange condition ($F_{1,11} = 18.32$, $p = 0.001$). The total rate of mutual positive interest across all conditions and outcomes was significantly higher in the NE Control than in the Token Exchange (Fig. 5).

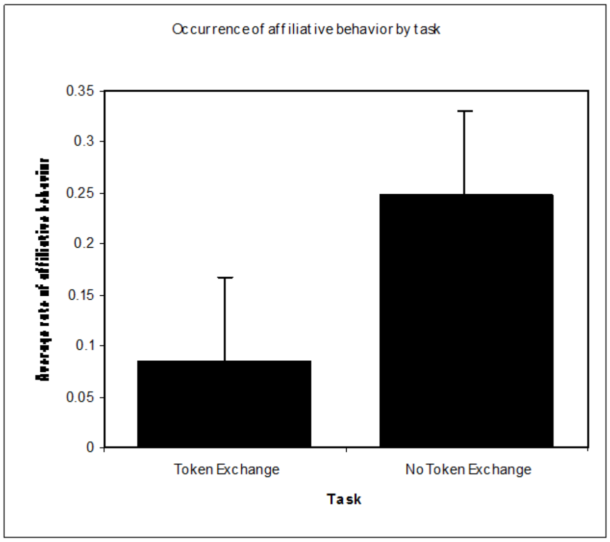

Figure 5. Overall rate of affiliative behavior in each exchange condition. Subjects exhibited higher rates of affiliative behavior during the NE Controls than during Token Exchange.

There was no significant difference in the rate of affiliative behavior during unequal and equal conditions ($F_{1,11}$ = 0.35, NS). Having an in-group or an out-group partner likewise did not effect the overall rate of affiliative behavior ($F_{1,11}$ = 0.35, NS). Finally, there were no significant interaction effects between any of the four factors.

Discussion

This study demonstrates that capuchin monkeys act more affiliatively while eating at the same time as another individual. Even when decision-making is removed, the rate of affiliative behavior following a dual-feeding outcome remains higher than that following a single-feeding outcome. This indicates that the act of choosing to benefit a conspecific is not what causes affiliative behavior to occur, but rather the act of eating together. Eating together can be the outcome of a choice by either one monkey or by the experimenter, and it seems that both stimulate affiliative behavior. If choice were a factor, then the difference in affiliative behavior between a prosocial and selfish outcome demonstrated by both de Waal et al. (2008) and Suchak (2010) would likely be a result of "warm glow" conferred on the actor by helping another individual. By eliminating decision-making, the opportunity for "warm glow" would likewise be eliminated, causing the distinction between prosocial and selfish outcomes to disappear.

Our data rather support the social eating hypothesis, our alternate hypothesis. Because the rate of affiliative behavior following a prosocial outcome was significantly higher than the rate following a selfish outcome after the decision-making was removed, the most likely explanation for the difference in affiliative behavior is that the prosocial outcome confers a reward to both individuals while the selfish outcome only rewards the actor. The increase in affiliative behavior when two rewards are present could be facilitated by a desire to maintain social interactions and closeness while eating (de Waal, Luttrell, & Canfield, 1993). Moreover, the increase could be reflective of positive reinforcement from engaging in a gratifying activity with another individual as opposed to engaging in the activity alone. When only one reward was present, mutual interest may have decreased because the social aspect of eating together was eliminated. Thus, it can be inferred that capuchins are motivated in these instances to act prosocially because doing so allows them to avoid eating alone and to engage in affiliative behavior with a conspecific.

While the difference in rate of affiliative behavior between prosocial and selfish outcomes relates back to our original hypotheses, the additional finding that the overall tendency for affiliative behavior is higher in the NE Control was unexpected. The possible implications of this result are multi-faceted but point in a similar direction. First, the increase in rate of affiliative behavior upon removal of the exchange task suggests that it is not merely the presence of food that facilitates affiliative behavior as the supported social eating hypothesis suggests; rather, the circumstances under which the food is present are likewise impacting mutual affiliation overall. In this case, food is either rewarded for successful completion of a task (Token Exchange) or is simply made available for consumption (NE Control). It has previously been demonstrated that when food is provided contingent on task performance, capuchins spend more time focusing on the task and on its potential outcomes than when they are not able to manipulate reward distributions (Dindo & de Waal, 2007; Brosnan & de Waal, 2003). Together with our results, this implies that the act of decision-making does not facilitate affiliative behavior overall; rather, it can deter from it, probably by shifting the focus from social eating to task completion. This is likewise supported by the methodological differences separating the Token Exchange from the NE Control. Because direct experimenter interactions were eliminated in the NE Control, subjects no longer had to spend any amount of time orienting towards a task situated away from their partners. Rather, the entirety of the time used to complete the exchange in the Token Exchange could be used instead for engaging in affiliative behavior during the NE Control. Thus, the increase in the overall tendency to be prosocial during NE Control likely can be explained by two possibilities: the NE Control converts food as a reward to food as food or the Token Exchange physically limits the amount of time allotted for each pair to be affiliative.

The fact that no significant difference exists between the rate of affiliative behavior during the equal reward condition and that during the unequal reward condition could simply indicate that the behavior as a whole is not motivated by the type of reward present. This inference is supported by the finding of no interaction effects between outcome and reward type. Similarly, the lack of significant difference between overall rate of affiliative behavior when paired with an in-group partner and an out-group partner could indicate that who subjects are eating with does not affect the positive interactions from eating together. This inference is likewise supported by the finding of no interaction effects between outcome and partner. Altogether, the results on reward and partner effects and interactions are consistent with the findings from the current token exchange study (Suchak, 2010). Subjects were motivated to eat together, but they were not more motivated by particular individuals or rewards.

Despite the distant relationship between humans and New World monkeys, we find in capuchins and other primates an unmistakable link to the foundations of our behavior. By studying the mechanisms that motivate prosocial behavior in capuchins, insight is gained into the social, environmental, and biological pressures that mediate prosociality in humans. More importantly, researchers are beginning to recognize the importance in examining not just the ultimate, but the proximate, as well. In order to understand what causes us to behave prosocially in the moment, we should look to our evolutionary past, where we find that both closely and distantly related primates have developed a tendency to help others not unlike our own.

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