Is Socially-mediated Sharing Ape-Specific?

The Effects of Cooperation and of a Food Prime on Food Sharing in Cotton Top Tamarins (*Saguinus oedipus*)

Julie J. Neiworth,

Cara J. Sylvester,

Janice M. Hassett,

and Benjamin M. Basile,

Carleton College

Full address of corresponding author:

Julie J. Neiworth
Dept of Psychology
Carleton College
Northfield, MN 55057

Email: jneiwort@carleton.edu
Phone: 1-507-646-4372
FAX: 1-507-646-7005

Submitted to Developmental Psychobiology

August 2, 2002

ABSTRACT

Cotton top tamarins readily share food with family members. To determine whether food sharing is effected by social awareness and actions, 6 pairs of adult tamarins were presented trials requiring them to emit a response simultaneously to receive a reward, and then were presented a bowl of salient food for sharing. The percentage of time spent sharing food was measured, and compared to trials of the same duration and the same food but without cooperation required before them. Four adult pairs spent a significantly larger portion of their time sharing following the cooperative act. The increase could not be accounted for by reward-induced tolerance to share, for in Experiment 2, the same tamarin pairs did not show a significant increase in sharing following free rewards. Like capuchins in a prior study (de Waal & Berger, 2000), tamarins showed increased sharing following acts which were socially synchronized.

Word count: 146

Key Words: food sharing, reciprocity, cooperation, monkeys, tamarins

Is Socially-mediated Sharing Ape-Specific?

The Effects of Cooperation and of a Food Prime on Food Sharing in Cotton Top Tamarins (*Saguinus oedipus*)

Recent research in developmental psychology has supported the observation that children naturally share and cooperate when interacting in a situation that could result in conflict (i.e., the sharing of toys, or group play; Killen & Cords, 2002; Turiel, 2002). In an analysis of more than 2000 conversations between groups of 3-year olds with no adults present, Turiel (2002) found that the most common social interactions were in the form of exchanges, offerings, and negotiations. In humans, the understanding of the role of a partner in a task appears near age 2 (Brownell & Carriger, 1991). The ability to cooperate and share has been linked developmentally to Stage 6 sensorimotor development, and rests on fundamental social cognitive abilities such as self-other differentiation, mental score-keeping, and perspective taking (de Waal, 1989).

Sharing has been studied in primates in the form of food sharing, and is thought to uncover conditions of reciprocal altruism (Trivers, 1971). Active food sharing has been defined behaviorally as a 1) voluntary transfer of 2) defensible food items by 3) food-motivated individuals (McGrew & Feistner, 1992). All three characteristics have to be present in order for the behavior to qualify as food sharing. This is typically experimentally controlled by providing a high quality food (thus insuring that subjects are motivated) and a small item (thus insuring that the item is defensible by the partner holding it, if he or she chose to), and controlling the sharing environment such that food sharing is voluntary. The sharing of food comes at a cost to the animal with food, thus its demonstration suggests an evolved social practice of tolerance that benefits the group. Social and cognitive processing in the act of sharing are implicated if sharing occurs between particular pairs who have shared with each other before (de Waal, 2000; Rapaport, 2001), if sharing is effected by the age of the recipient (Rapaport, 2001; Feistner & Price, 1990), if sharing is influenced by the quality of the food (de Waal, 2000; Feistner & Chamove, 1986), and if sharing is influenced by social interactions that transpired before sharing (de Waal & Berger, 2000).

Generally, there is a lack of food sharing among primates, but consistent notable exceptions come from three distinct groups: 1) chimpanzees who share meat, fruit, and plants among adults (Boesch & Boesch, 1989; McGrew & Feistner, 1992; de Waal, 1989, 1992), 2) capuchins, new world monkeys who hunt and share squirrel (Rose, 1997) and coati pups (Perry & Rose, 1994) and 3) marmosets and tamarins, new world monkeys who share food within families (for golden lion tamarins, Brown & Mack, 1978; Rapaport, 2001; for cotton top tamarins, Feistner & Chamove, 1986; Feistner & Price, 1990). Of these three groups, only capuchins and chimpanzees have been studied further to determine their understanding of cooperation, and its relationship with food sharing. If food sharing is an act in which the participants have an awareness of their social partner and voluntarily share, then one would expect animals who actively share food to also understand and react appropriately in a task involving cooperation. In research in the laboratory, cooperation has referred to the performing of a simultaneous action by two animals to acquire a reward (for example, Chalmeau, Lardeux, Brandibas & Gallo, 1996; Chalmeau & Gallo, 1996; de Waal & Berger, 2000; Visalberghi, Quarantotti, & Tranchida, 2000).

An early documented act of sharing among chimpanzees involved young chimpanzees sharing items through the bars of cages (Nissen & Crawford, 1936). The sharing that transpired seemed to involve score keeping, in that it was influenced by both parties sharing with the other. de Waal (1989) found similar results in plant sharing among chimpanzees. He found a positive relationship between given and received acts of plant sharing which he interpreted to indicate reciprocal altruism. In the field, sharing of food has been documented in bonobos and traditional chimpanzees (Goodall, 1963; Boesch & Boesch, 1989).

Successful cooperation has been documented consistently in chimpanzees, both in the wild (i.e., in hunting, Boesch & Boesch, 1989. 2000; Stanford, 1998; and in ladder climbing, Menzel, 1972), and in the laboratory (Savage-Rumbaugh, Rumbaugh, & Boysen, 1978; Chalmeau, 1994; Chalmeau & Gallo, 1996). The laboratory experiments required two chimpanzees to work together to acquire food, and resulted in significant correlations between the two partners' behaviors, and more social vigilant behaviors such as increased glancing at the partner, and looking more often when the partner approached the apparatus that needed manipulation to acquire food. More recently, positive results were obtained from 2 orangutans in a similar study requiring simultaneous actions (Chalmeau, Lardeux, Brandibas & Gallo, 1996). It is tempting from this work to conclude that the understanding of the partner's role in a cooperative situation, and potentially the active sharing of a significant item with another, is an ability specific to great apes, and one that requires fairly sophisticated social awareness and cognitive competence. An alternative is that particular species of monkeys who show active food sharing, the capuchins and the tamarin/marmoset groups, are also aware of social partners and may act reciprocally.

Capuchins have been observed to share among adults, and to exchange both edible and inedible objects among adults (Thierry, Wunderlich & Gueth, 1989; de Waal, Luttrell, & Canfield, 1993). In a study of unrelated female pairs, de Waal (2000) found that capuchins' food sharing rates were based on prior incidents of food sharing between pairs, with a history of sharing increasing the rate of food sharing. Moreover, de Waal found that higher quality food items led to a decrease in the rate of the possessor to share food with a recipient. While these studies document factors which influence food-sharing among capuchins, they do not reveal whether social thinking may be involved in the act. A study by de Waal & Berger (2000) which combined cooperation and food sharing found that capuchin pairs' rate of food sharing, in the form of facilitated taking or dropping food near where another could get access to it, increased if the pair had previously worked in a cooperative task involving the simultaneous pulling of a handle for one of them to gain access to a bowl of food. Food sharing following cooperation was significantly higher than food sharing in a solo condition wherein one individual of the pair acted alone to gain access to the bowl of food. The authors concluded that the increase in sharing following cooperation may show mental score-keeping, a specific brand of reciprocity based on past social events. Alternatively, they contend that the cooperative task may have brought on an elevated attitude which led to increased sharing and tolerance, a state de Waal (2000) called "attitudinal reciprocity". In sum, capuchins shared rewards more readily after a joint effort than when the rewards were obtained individually. This implies that an awareness of the social situation and collaboration influenced food sharing, and thus that food sharing is a more active, socially mediated process in capuchins.

In contrast, capuchins have consistently shown a lack of understanding of a partner's role in a cooperative task. While Chalmeau, Visalberghi and Gallo (1997) found that tufted capuchins successfully worked in pairs to pull handles together to gain access to food, they found that the monkeys did not pull more frequently when a partner was close to the handle than when the partner was far away. In a follow-up study with more reliably matched pairs and more obvious manipulative actions for the pairs to perform, Visalberghi, Quarantotti, and Tranchida (2000) found that capuchins' pulling rate was not affected by the partner's behavior, and was only weakly affected by the partner's spatial position to the handle. So, while capuchins appear to cooperate successfully in the laboratory, it is also clear that their responses are not mediated by the partner's actions. It is possible that capuchins' natural tendency toward exploratory behavior (Tomasello & Call, 1997) led to higher frequencies of pulling responses in the task which, coincidentally, occurred while a partner was also emitting the response. Alternatively, it might be the case that capuchins cannot inhibit a pulling response once it has been rewarded, and thus pull the handle even in conditions that will be unsuccessful. A lack of response inhibition has been documented in another new world monkey, the tamarin (Santos, Ericson & Hauser, 1999) and in old world monkeys, specifically, rhesus macaques (Thompson & Oden, 1996). Two different species of macaques also failed to inhibit a response in a cooperative task that required pairs to push a boulder together to acquire food (Petit, Desportes & Thierry, 1992). Because many species of monkeys have difficulty inhibiting a ready response which has led to prior reinforcement, a demonstration of social thinking in cooperative tasks which rests on greater responding occurring with a partner than separately may be incompatible with their behavioral tendencies. There is a great advantage in tapping into a different set of behaviors to measure the social awareness induced by a cooperative effort, and de Waal and Berger (2000) showed that food sharing behaviors peaked following a cooperative task in capuchins.

A critical test in determining the generality of sharing and cooperation in primates is to examine the effect of cooperation in another species of monkey known to show active food sharing. The sharing of food among tamarins occurs at high frequency in family groups, between older individuals and younger ones, and between older siblings (Feistner & Price, 1990). Among golden lion tamarins, mental score-keeping over a period of weeks does not account for food transfers, thus food sharing seems to act more on mutualism (Rapaport, 2001). Salient food stuffs increase the rate of food sharing among cotton top tamarins (Feistner & Chamove, 1986). The findings that tamarins share among their social group, that they favor sharing with the young, and that better quality food motivates them to share more implies an active cognitive processing of sharing with an assessment of receiver and of food quality as factors in the act. Still, it is possible that the sharing of food occurs as a function of kinship and development, and that eating primes tolerance toward others. If that is the psychological mechanism at work, very little social awareness or cognitive work is needed to produce increased food sharing, other than a high quality food item as a prime.

What is needed is a study of the effects of cooperation on food sharing among families of tamarins. If in members of this species, there is social and cognitive processing in food sharing, then a preceding act of cooperation should lead to an increase in food sharing beyond that measured to the same food stuffs and between the same partners when cooperation/collaboration is not required.

This experiment tests for the existence of social awareness and cognitive mediation in food sharing in tamarins. Three conditions are conducted, and food sharing across them is compared directly. In a control condition, family pairs are given 25 trials of 1-minute access to a high quality food, and the rate of tolerated food sharing is measured. In a cooperative condition, the same pairs are first required to emit a response simultaneously to obtain a high quality food item, and then are allowed to share food in 1-minute trials. To control for the effect of the food item acting as a prime for food sharing, a second experiment exposed the pairs to a food prime condition in which each pair was given a single high quality food item, and then allowed to share food in 1-minute trials. If cooperation leads to increased tolerance and food sharing, then the cooperation condition should generate more food sharing than the other conditions. However, if high quality foods which are coincidentally also obtained for cooperating but obtained freely in the food prime condition generate increased tolerance and food sharing because eating primes the animals to tolerate each other more, then both the cooperative condition and the food prime condition will generate more food sharing behavior than the control condition.

Experiment 1

Methods

Subjects

Eleven adult captive-born cotton-top tamarins (*Saguinus oedipus*) served as subjects forming 6 family pairs in this study. The relationships among tested pairs were mother-son for Caitlin and Dante, and Caitlin and Sebastian, siblings for Rolo and Yohoo, and Ophelia and Olympia, and mated pairs for Fozzie and Zhivago and Mac and Oprah. Four of the pairs involved female-male dyads (Caitlin and Dante, Caitlin and Sebastian, Fozzie and Zhivago, and Mac and Oprah), while the sibling pairs consisted of same-sex dyads, one female (Ophelia and Olympia) and one male (Rolo and Yohoo). The four pairs who were either mated pairs or siblings lived as pairs and were tested in their home cage. The pairs consisting of the mother Caitlin and her two sons were tested as pairs separately in a group cage which housed them. All subjects were of adult age, with age varying from 3 to 12. All subjects had been nursery-peer reared in lab settings and had been socially housed since December, 1998.

The subjects had been involved in the following experiments: tests with a mirror for evidence of self-awareness (Neiworth, Anders, & Parsons, 2001), gaze direction tests involving object choice (Neiworth, Burman, Basile, and Lickteig, 2002), and a test of object permanence involving object choice. In the latter two experiments, subjects had been trained individually to sit on a cart in front of an apparatus and make a cup-tipping response to earn a food reward. Prior to the experiment in this paper, there was no training of actions done together among any of the subjects.

Subjects were tested in their home cages. The pairs were housed in 0.85m X 1.5m X 2.3m cages, separated by opaque sheets. The family was housed in a 1.8m X 3.0m X 2.3m cage. The subjects were on a 12-hour light/dark schedule and had free access to water. Their daily diet consisted of a yogurt and applesauce breakfast, a main feed of Zupreem Marmoset chow, Mazuri New World Monkey dry chow, fruits and vegetables, and an afternoon protein snack (e.g. eggs, hamburger, peanuts).

Apparatus

For Cooperation trials (see Procedure), two wood stands approximately 10cm in height with 18 X 18 cm surfaces were placed on a cart measuring 117cm in height with a 40 X 50 cm top.

The food used throughout this experiment consisted of pieces of fruit sugar cereal (specifically, Kellogg's® Fruit Loops), a highly desirable food for the tamarins that had served successfully to motivate responses in prior studies. The cereal was placed in the regular main feed bowl measuring 6cm in height and 20cm in diameter. The bowl was placed on a wall-mounted food shelf measuring 26.5 X 26.5cm, which was permanently fixed in the subjects' cages and visited in the past during meal times.

Procedure

The procedure consisted of a pre-training phase during which the subjects were trained to perform a cooperative simultaneous response on the cart apparatus, and a test phase in which subjects were exposed in counterbalanced order across pairs to a control condition and a cooperation condition. The cooperative response was pre-trained so that it could be executed consistently in the test phase just before each food-sharing trial. Each phase is described below. Food-sharing behavior was the dependent variable, and active food sharing was determined by the experimental design because the subjects had shown strong motivation to acquire the food items used, and the food items were small and defendable by individuals. The food sharing environment was the food shelf used in the animals' home cage, thus any sharing was voluntary. The data analyzed were the percentage of total time in each trial that was spent engaged in food-sharing behavior, and this was calculated per session for each pair within each test (control and cooperation).

Pre-Training

In pre-training, all subject pairs were shaped to climb onto the cart and sit together on the wood stands. One experimenter always stood within 0.33 m of the cart and wood stand apparatus during pre-training. This experimenter called subjects by name, indicated with pointing and looking gestures the location the subjects should approach, and provided reinforcement in the form of fruit cereal for appropriate responses. The pre-training was accomplished in steps, with the criterion that an appropriate response was emitted 3 consecutive times before subjects were challenged with the next step. In the initial step of shaping, the pair of subjects were given auditory cues using their names, and an experimenter pointed to the cart to indicate the location they should approach. Cereal reinforcers were placed on the wood stands on the carts, and subjects could acquire them by approaching and sitting on the cart. Next, the cereal reinforcers were made visible only after either subject came onto the stands. Finally, reinforcement was offered only when subjects were on the stands at exactly the same time. This final behavior, of the pairs sitting in close proximity on each of the two wood stands on the cart simultaneously, was the cooperation manipulation. Sessions were conducted lasting 30 minutes per pair. The shaping was accomplished for all pairs within 5-8 consecutive pre-training sessions.

Testing

The Control and Cooperation conditions were administered in a counterbalanced order, with half of the pairs exposed to the control condition first

(Dante (with Caitlin), Ophelia/Olympia, Rolo/Yohoo) and half of the pairs exposed to the cooperation condition first (Fozzy/Zhivago, Mac/Oprah, Sebastian (with Caitlin)). Each condition consisted of 5 sessions conducted consecutively, with each session consisting of 5 trials. Sessions were conducted immediately before the delivery of the pairs' daily main feed.

Control Condition. In this condition and for each trial, food sharing behavior, defined as both animals sitting with both back legs on the food shelf, was timed over a 60-second interval. Each trial began with one experimenter placing cereal (typically 5 – 10 pieces) in the pairs' normal main feed bowl. The bowl was then placed on the food shelf and the experimenter either left the cage or went to the opposite end of the cage. Timing of the trial began when either of the two subjects of the pair sat on the food shelf. Of the total 60 seconds, the times that both subjects simultaneously shared the food shelf were recorded as food sharing behavior. In almost all cases, when the subjects were both on the shelf, they were also both engaged in eating the fruit cereal. Times were recorded using a hand-held stopwatch, and the food sharing time was started when 2 animals were both on the shelf, and was terminated when either animal left the shelf, defined as both hind legs removed from the shelf. At the end of each trial the bowl was removed from the food shelf and a 60-second intertrial interval was presented, during which time the experimenters disengaged any contact from the subjects. A total of 5 trials were conducted per session, with 5 consecutive sessions administered. Trials in which the food cereal was presented but no animal approached the bowl (and thus the 60-second time period was not initiated) were aborted after 3 minutes of food exposure.

For subjects housed in pairs and tested as pairs, the sharing behavior that occurred between each pair was collected. For subjects housed in the group cage (Caitlin, Dante, and Sebastian), food sharing behavior was coded using the two siblings (Dante and Sebastian) as the focal animals. That is, any sharing between one of the two focal animals and any other animal in the cage constituted food sharing behavior for the focal animal being studied. This meant that there was an increased chance of food sharing in the group cage because more animals were present, however this increase was true of both conditions and thus would not bias the results in favor of either condition.

Cooperation Condition. There were 5 consecutive sessions conducted, with 5 trials per session in this condition as well. Each trial started with a requirement that both animals of the pair perform the simultaneous wood stand-sitting response (see Figure 1 for an example.). An experimenter stood within 0.33 m of the cart and called each subject of a pair over to the cart to emit this response. Once both subjects were simultaneously seated on the two wood stands, a single food reward was given simultaneously to each of the pair. This requirement took varying lengths of time, from 10 seconds to approximately 2 minutes per trial. The experimenter would wait until both subjects had eaten the single food rewards, and then each trial would progress exactly as was done in the control condition (in terms of baiting the main feed bowl and timing the 60-second interval). The dependent variable was food-sharing behavior, defined the same as was described in the control condition.

As in the control condition, for subjects housed in pairs and tested as pairs, the sharing behavior that occurred between each pair was collected following each pairs' successful completion of the cooperative task. For subjects housed as a group, the requirement of cooperation was exerted on the pair named (Caitlin with Dante, or Caitlin with Sebastian). Following this cooperative task, food sharing behavior was collected when it occurred between the sibling focal animal (Dante or Sebastian) and any other subject in the group cage. This meant that for the group, there were increased chances of food sharing with increased members in the test environment. This increase was true in both conditions, however, and thus did not bias the data collection toward either condition.

RESULTS

The food-sharing times were used to determine the percentage of total time in each trial spent sharing food. A single total percent score for each session for each pair was used in subsequent analyses. When 6 pairs were included in the analyses, and both fixed and repeated measures were involved, parametric tests using SPSS were conducted. Those tests which involved 4 pairs of subjects and repeated measures were subjected to nonparametric tests in SPSS. An alpha level of 0.05 was used for significance.

One noticeable effect in the study was significant variability between the subject pairs in terms of how much time was spent engaged in food-sharing behavior. The dependent variable, the total percentage of time per session (out of 300 seconds) spent exhibiting food-sharing behavior for each of 5 sessions in each condition, was analyzed in a mixed model analysis of variance (ANOVA), with the repeated measure condition (Control vs. Cooperation) and the fixed factor subject pair (n of 6 pairs) as the independent variables. The result was a significant subject main effect ($F (5,24) = 4.77$, $p < 0.01$) and a significant subject X condition interaction ($F (5,24) = 3.22$, $p = 0.02$). The condition main effect was not significant ($p=0.15$). Figure 2 shows the significant subject X condition effect. For 4 pairs, depicted on the left side of Figure 2, the control condition generated less food-sharing behavior (median = 9.56% of the time) than the cooperation condition (median =20.80% of the time). For these 4 pairs, the difference between the control and cooperation conditions was significant, as analyzed by a nonparametric Wilcoxon signed ranks test for repeated measures (estimated $Z = -2.95$, $p < 0.01$). For the other 2 pairs, graphed on the right side of Figure 2, the two conditions were not significantly different from each other, and showed slightly increased food-sharing in the control condition. The difference in behaviors between the 4 pairs who showed a significant effect of condition on their behavior and the 2 who did not show the effect accounted for the significant interaction between subject pair and condition.

A separate mixed model ANOVA was conducted to examine the fixed factor order of condition (control first or cooperation first) and the repeated measure condition (control and cooperation) on the same food-sharing data. It was thought that there might be elevated food-sharing behavior as a function of practice in the task, and thus the 2^{nd} condition presented (whether control or cooperation) might generate more food-sharing behavior than the 1^{st} condition presented. There was a significant order X condition interaction effect ($F(1, 28) = 6.70$, $p=0.015$), and the interaction is depicted in Figure 3. The main effect condition and the main effect order were not significant. The significant interaction effect revealed an interesting effect of order. First, it is clear from the interaction that the cooperation condition generated similar levels of food-sharing behavior whether it was presented as the first condition (mean = 16.31%) or the second condition (mean =17.90%). In contrast, the control condition generated significantly more food-sharing behavior when it was presented second (mean =19.14%) than first (mean = 8.57%), and this was confirmed by an independent samples t-test ($t(28) = -3.73$, $p < 0.01$). When the control condition was the first condition presented, it generated much less food-sharing behavior than the cooperation condition when it was presented first, and this resulted in a trend difference between the two first conditions ($t(28) = -1.82$, $p = 0.08$). The other differences, between cooperation presented first or second, or between either condition presented second, were not significantly different.

DISCUSSION

The general result was that 4 subject pairs showed significantly elevated food-sharing behavior following a task in which they had to perform an act simultaneously, as compared to a control condition in which they were allowed the same amount of time and the same type of food to share. This result was not accounted for by a practice effect for the effect of cooperation; in fact the level of food-sharing behavior following a cooperative task was similar regardless of whether the condition was presented first or second. There was an effect of practice on the level of food sharing exhibited in the control condition, for if that condition was presented second, it generated significantly elevated food-sharing behavior. The elevated food sharing noted to occur with practice in the control condition implicates that food delivery itself and an expectation of food may increase food-sharing in primates, and this effect is not related to social and cognitive processing of the sharing event per se.

EXPERIMENT 2: FOOD PRIME CONTROL

Taken together, the data could be interpreted to indicate that social awareness prompted by the simultaneous requirement of activity between the subject pairs caused an increased tolerance at the food dish for most pairs. An alternative possibility is that the administration of a food reward (coincidentally, for cooperating) induced the increased tolerance at the food dish. In social psychology, such a manipulation is thought to elevate mood in people, and may cause people to be more willing to help others or to share. In studies of tamarin food-sharing, it was observed that salient foods induced increased food-sharing among families, especially between older members and younger ones (Feistner & Chamove, 1986). It is possible in this design that the delivery of a reinforcement at the end of the social activity served to prime subjects to share more, either because motivation and/or mood was elevated, or because food-sharing itself is primed by salient foodstuffs, but not because something socially mediated occurred which was later considered within the food-sharing event. This alternative was examined in the final experiment, in which subject pairs for whom cooperation seemed to elevate food sharing were now given a salient food item as a prime before a “control” condition was conducted. On each trial, food reinforcers were given to each subject in each pair, and then food-sharing behavior was coded for 60 seconds, as was done in the former control condition. If the food item primed subjects to share food more, then there should be elevated food-sharing behavior comparable to that seen in the cooperation condition.

Experiment 2

Methods

Subjects

The 4 pairs of subjects from Experiment 1 who showed a difference in food sharing behavior as a function of cooperation were used.

Apparatus

The same fruit cereal served as the food prime and as the food items in the food-sharing trials. The cart and stands were not used. The food shelf used in Experiment 1 served as the location for food sharing in Experiment 2 as well.

Procedure

There were 5 consecutive daily sessions conducted, with 5 trials per session. Before each trial began, an experimenter stood within reach of the food shelf and called each subject of a pair over to acquire a food reward. A single food reward was given to each subject, but there was no attempt to do this simultaneously, and in fact, typically subjects received the food cereal serially. The experimenter would then wait until both subjects had eaten the single food rewards, and then each trial would progress exactly as was done in the control condition in Experiment 1 (in terms of baiting the main feed bowl and timing the 60-second interval). The dependent variable was food-sharing behavior, defined the same as in Experiment 1.

For subjects housed in pairs and tested as pairs, the pair studied received the prime food item, and then the sharing behavior that occurred between each pair was coded. For subjects housed as a group, the two subjects involved in the prior cooperation task (Caitlin and Dante, and Caitlin and Sebastian) were given the food prime, and then food sharing behavior was collected when it occurred between the sibling focal animal (Dante or Sebastian) and any other subject in the group cage. This meant that for the group, there were increased chances of food sharing with increased members in the test environment. This increase was true in prior conditions as well.

Results

The food sharing times were used to determine the percentage of total time for each 5-trial session that was spent sharing food. Nonparametric tests were used, since the sample size was 4 subject pairs. The alpha level was set at 0.05 for significance for all tests.

A repeated measures Friedman's ANOVA comparing the three conditions (Control, Cooperation, and Food Prime) across the subject pairs revealed a significant condition effect (χ^2 (20) = 6.70, p = 0.035). Figure 4 depicts the medians of the conditions. The pattern shown was that food primes elevated food sharing behavior (median = 12.56%) above that shown in the control condition (median = 9.56%), but not to the level observed following cooperation (median = 20.80%). Pairwise comparisons using nonparametric Wilcoxon signed ranks tests confirmed again that food-sharing was significantly increased in the cooperation condition as compared to the control condition (estimated Z = -2.95, p<0.01), but there was no significant difference between food sharing in the control and food prime conditions (p=0.575) nor between the food prime and the cooperation conditions (p=0.11), although this comparison approached the level of a trend.

General Discussion

In many prior studies of primate cooperation, two animals have been required to execute an act simultaneously (e.g., both pull separate handles) to acquire reinforcement. The cooperative act here was less direct. The requirement was for two animals to both climb to two different locations and sit on stands simultaneously to get reinforced. While the action required here is quite different from those of past studies, both types of tasks require social awareness in terms of timing a behavior with a partner to generate rewards. Because tamarins have already demonstrated a lack of ability to inhibit ready responses even if reinforcement is withheld for emitting them (Santos, Ericson and Hauser, 1999), it seemed unlikely that tamarin pairs would be able to selectively emit responses in pairs at a rate higher than they might do individually. Still, if they were able to attend to a partner’s actions, any act requiring social mediation and timing should increase social awareness. And, if food sharing is an act mediated by social awareness in tamarins, then a condition which peaks tamarins’ awareness of others via a prior joint act should increase food sharing. An effect of social awareness on food sharing was in fact demonstrated in tamarins’ behavior.

In this set of experiments, adult tamarins in family pairs showed increased food sharing when they participated in an act requiring simultaneous execution just before the food-sharing opportunity. The increased sharing was significantly higher than a control condition in which the same salient food items were offered to the same pairs for the same lengths of time. The act of eating salient foods before sharing could not account for the elevated sharing in the cooperation condition. This was confirmed in Experiment 2 in which a salient food was offered as a prime before the same food-sharing opportunity. Under this condition, sharing was increased slightly above the control condition, but was still lower than that observed after cooperation and the difference between priming and cooperation produced a marginal trend ($p=0.11$).

The act of cooperating seemed especially powerful as an agent to induce increased sharing, beyond that of any elevated attitude brought on by a salient reward obtained freely. An indication of the power of cooperation to tune animals into each other was revealed by the significant order X condition effect found in

Experiment 1. That finding revealed that animals first given 25 trials in which cooperation was required over a 5-day period showed two unique behaviors: 1) elevated food sharing following each cooperative trial, and 2) elevated food sharing in their subsequent food sharing control condition. There was not a general effect of practice in that second conditions generated more food-sharing than first conditions. In contrast, when cooperation was required first for 5 sessions, food sharing remained elevated throughout the subsequent second control condition. This effect implies that the cognitive processing about a partner's actions that occurred in the cooperation condition may have continued to exert an influence in later food sharing opportunities.

This study suggests strong social mediation of sharing in another new world monkey species who actively share food among families, the cotton top tamarin. Together with the other species of primates who actively share, capuchins and chimpanzees, the tamarins studied here demonstrated that cooperative acts are socially and cognitive processed because they influence rates of later sharing. Like the capuchins in the study by de Waal & Berger (2000), the tamarins showed increased food sharing following acts which were socially synchronized. Socially mediated sharing is not specific to apes, but rather seems to be an outcome shared by the primate species who share food in natural settings.

Author Notes

All correspondence concerning this article should be sent to Julie J. Neiworth, Department of Psychology, Carleton College, Northfield, MN 55057, email jneiwort@carleton.edu. The authors would like to thank Charles Snowdon, Departments of Psychology and Biology, University of Wisconsin-Madison, for the generous gift of animals to Carleton College, and to Carleton College and to the Howard Hughes Medical Institute for its support of this project. The experiment herein complies with the standards for care and research in the US, as described by USDA and according to NIH's Guide for the Care and Use of Laboratory Animals (1996), and was approved by Carleton College's Institutional Animal Care and Use Committee (IACUC).

References

Boesch, C. & Boesch, H. (1989). Hunting behaviour of wild chimpanzees in the Tai National Park. American Journal of Physical Anthropology, 78, 547-573.

Boesch, C. & Boesch, H. (2000). The Chimpanzees of the Tai: Behavioural Ecology and Evolution. Oxford, England: Oxford University Press.

Brown, K. & Mack, D.S. (1978). Food sharing among captive *Leontopithecus rosalia*. Folia Primatologica, 29, 243-251.

Brownell, C.A., & Carriger, M. S. (1991). Collaborations among toddler peers: Individual contributions to social contexts. In Perspectives on Socially Shared Cognition. Washington, DC, US : American Psychological Association, pp. 365-383.

Chalmeau, R., & Gallo, A. (1996). What chimpanzees (*Pan troglodytes*) learn in a cooperative task. Primates, 37, 39-47.

Chalmeau, R., Visalberghi, E. & Gallo, A. (1997). Capuchin monkeys, *Cebus apella*, fail to understand a cooperative task. Animal Behaviour, 54, 1215-1225.

Chalmeau, R., Lardeaux, K., Brandibas, P., & Gallo, A. (1997). Cooperative problem solving by orangutans (*Pongo pygmaeus*). International Journal of Primatology, 18(1), 23-32.

de Waal, F.B.M. (1989). Food-sharing and reciprocal obligations among chimpanzees. Journal of Human Evolution, 18, 433-459.

de Waal, F.B.M. (1992). Appeasement, celebration and food sharing in the two *Pan* species. In Topics in Primatology: Vol. 1, Human Origins, (Ed by T. Nishida, W.C. McGrew, P. Marler, M. Pickford, & F.B. de Waal), pp. 37-50. Tokyo, Japan: University of Tokyo Press.

de Waal, F.B.M., Luttrell, L.M. & Canfield, M.E. (1993). Preliminary data on voluntary food-sharing in brown capuchin monkeys. American Journal of Primatology, 43, 33-41.

de Waal, F.B.M. & Berger, M.L. (2000). Payment for labour in monkeys. Nature, 404, 563.

de Waal, F. B. M. (2000). Attitudinal reciprocity in food sharing among brown capuchin monkeys. Animal Behavior, 60, 253-261.

Feistner, A. T., & Chamove, A. S. (1986). High motivation toward food increases food-sharing in cotton-top tamarins. Developmental Psychobiology, 19, 439-452.

Feistner, A. T., & Price, E. D. (1990). Food-sharing in cotton-top tamarins (*Saguinus oedipus*). Folia Primatologica, 54, 34-45.

Goodall, J. (1963). My life among wild chimpanzees. National Geographic, 124, 272-308.

Killen, M. & Cords, M. (2002). Prince Kropotkin's ghost. American Scientist, 90, 208-210.

McGrew, W.C. & Feistner, A.T.C. (1992). Two nonhuman primate models for the evolution of human food sharing: Chimpanzees and callitrichids. In The Adapted Mind: Evolutionary Psychology and the Generation of Culture, London, England: Oxford University Press, pp. 229-243.

Menzel, E.W. (1972). Spontaneous invention of ladders in a group of young chimpanzees. Folia Primatologica, 17, 87-106.

Neiworth, J. J., Anders, S. L., and Parsons, R. R. (2001). Tracking responses related to self-recognition: A frequency comparison of responses to mirrors, photographs, and videotapes by cotton top tamarins (*Saguinus oedipus*). Journal of Comparative Psychology, 115, 432-438.

Neiworth, J. J., Burman, M. A., Basile, B. M., and Lickteig, M. T. (2002). Use of experimenter-given cues in visual co-orienting and in an object-choice task by a New World monkey species, Cotton Top Tamarins (*Saguinus oedipus*). Journal of Comparative Psychology, 116, 3-11.

Nissen, H. & Crawford, M. (1936). A preliminary study of food-sharing behaviour in young chimpanzees. Journal of Comparative Psychology, 22, 383-419.

Perry, S. & Rose, L. (1994). Begging and transfer of coati meat by white-faced capuchin monkeys, *Cebus capucinus*. Primates, 35, 409-415.

Petit, O., Desportes, C. & Thierry, B. (1992). Differential probability of “coproduction” in two species of macaque (*Macaca tonkeana, Macaca mulatta*). Ethology, 90, 107-120.

Rapaport, L.G. (2001). Food transfer among adult lion tamarins: Mutualism, reciprocity or one-sided relationships? International Journal of Primatology, 22, 611-629.

Rose, L. (1997). Vertebrate predation and food-sharing in *Cebus* and *Pan*. International Journal of Primatology, 18, 727-765.

Santos, L.R., Ericson, B.N., and Hauser, M. D. (1999). Constraints on problem solving and inhibition: Object retrieval in cotton top tamarins (*Saguinus oedipus oedipus*). Journal of Comparative Psychology, 113, 186-193.

Savage-Rumbaugh, E.S., Rumbaugh, D.M., & Boysen, S. (1978). Linguistically mediated tool use and exchange by chimpanzees (*Pan troglodytes*). Behavioral and Brain Sciences, 4, 539-554.

Stanford, C.B. (1998). Chimpanzee and Red Colobus: The Ecology of Predator and Prey. Cambridge, MA: Harvard University Press.

Thierry, B., Wunderlich, D. & Gueth, C. (1989). Possession and transfer of objects in a group of brown capuchins (*Cebus apella*). Behaviour, 110, 294-305.

Thompson, R. K. R., & Oden, D. L. (1996). A profound disparity revisited: Perception and judgment of abstract identity relations by chimpanzees, human infants, and monkeys. Behavioural Processes, 35, 149-161.

Tomasello, M. & Call, J. (1997). Primate Cognition. New York, NY, US: Oxford University Press.

Trivers, R.L. (1971). The evolution of reciprocal altruism. Quarterly Review of Biology, 46, 35-57.

Turiel, E. (2002). The Culture of Morality: Social Development, Context, and Conflict. New York, NY, US : Cambridge University Press.

Visalberghi, E., Quarantotti, B. P. & Tranchida, F. (2000). Solving a cooperation task without taking into account the partner's behavior: The case of capuchin monkeys (*Cebus apella*). Journal of Comparative Psychology, 114, 297-301.

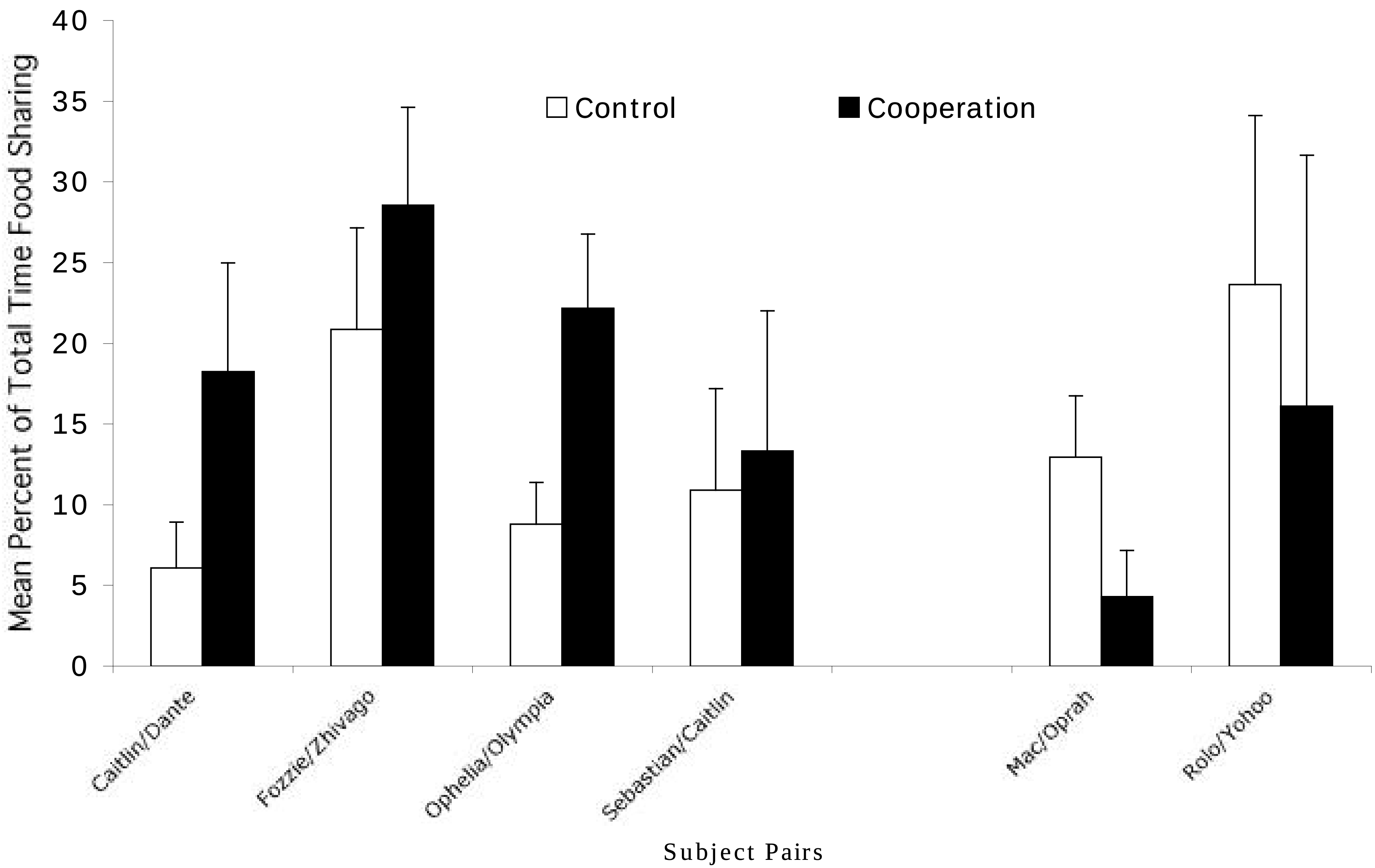
Figure Captions

Figure 1. A subject pair in the cooperation condition. The two subjects (brothers Rolo and Yohoo) had to sit on two wood stands simultaneously to receive a reward.

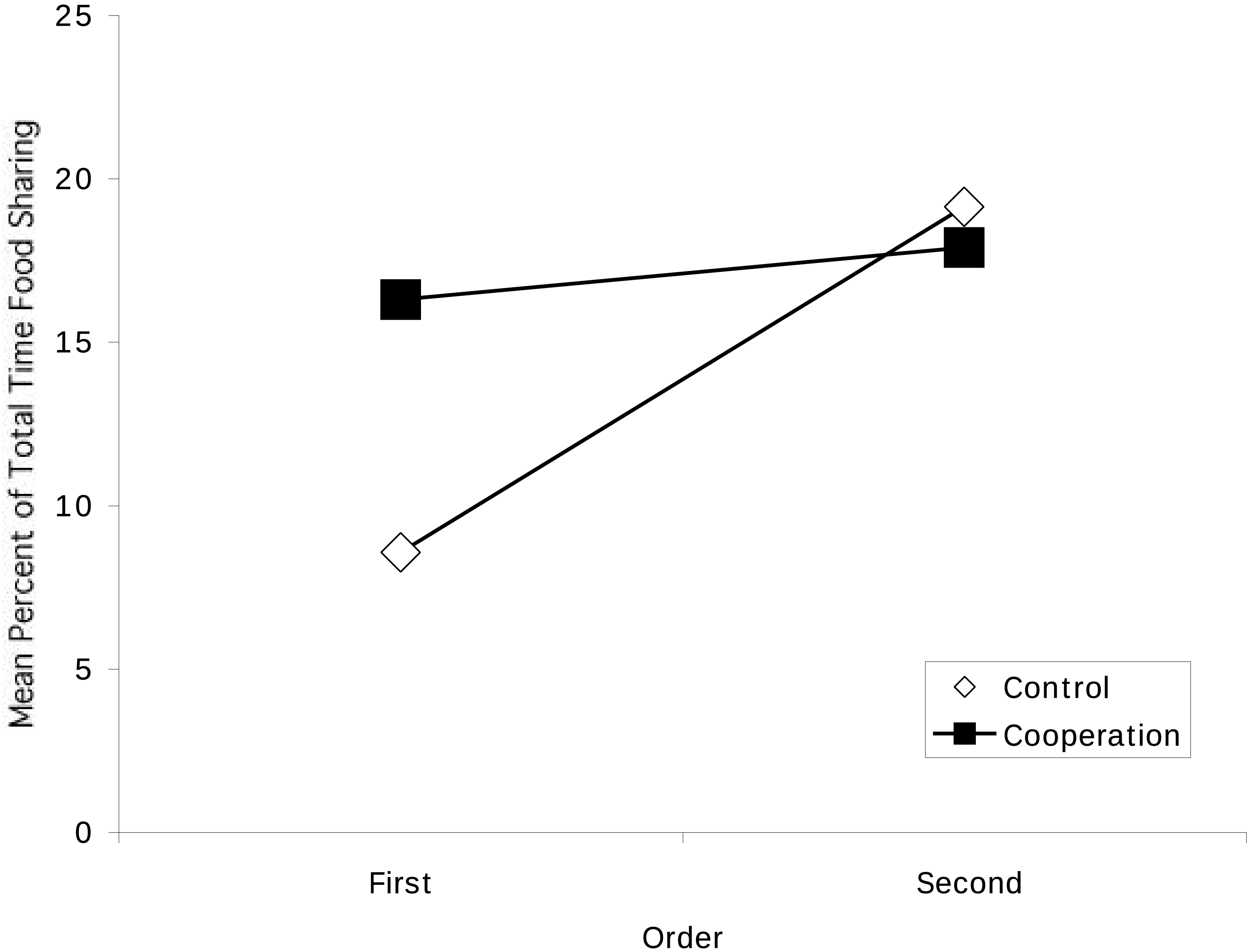
Figure 2. Averaged percentage of total time spent food sharing in the cooperation and control conditions by subject pair.

Figure 3. Averaged percentage of total time spent food sharing in the first and second conditions presented, separated by the type of condition (control or cooperation).

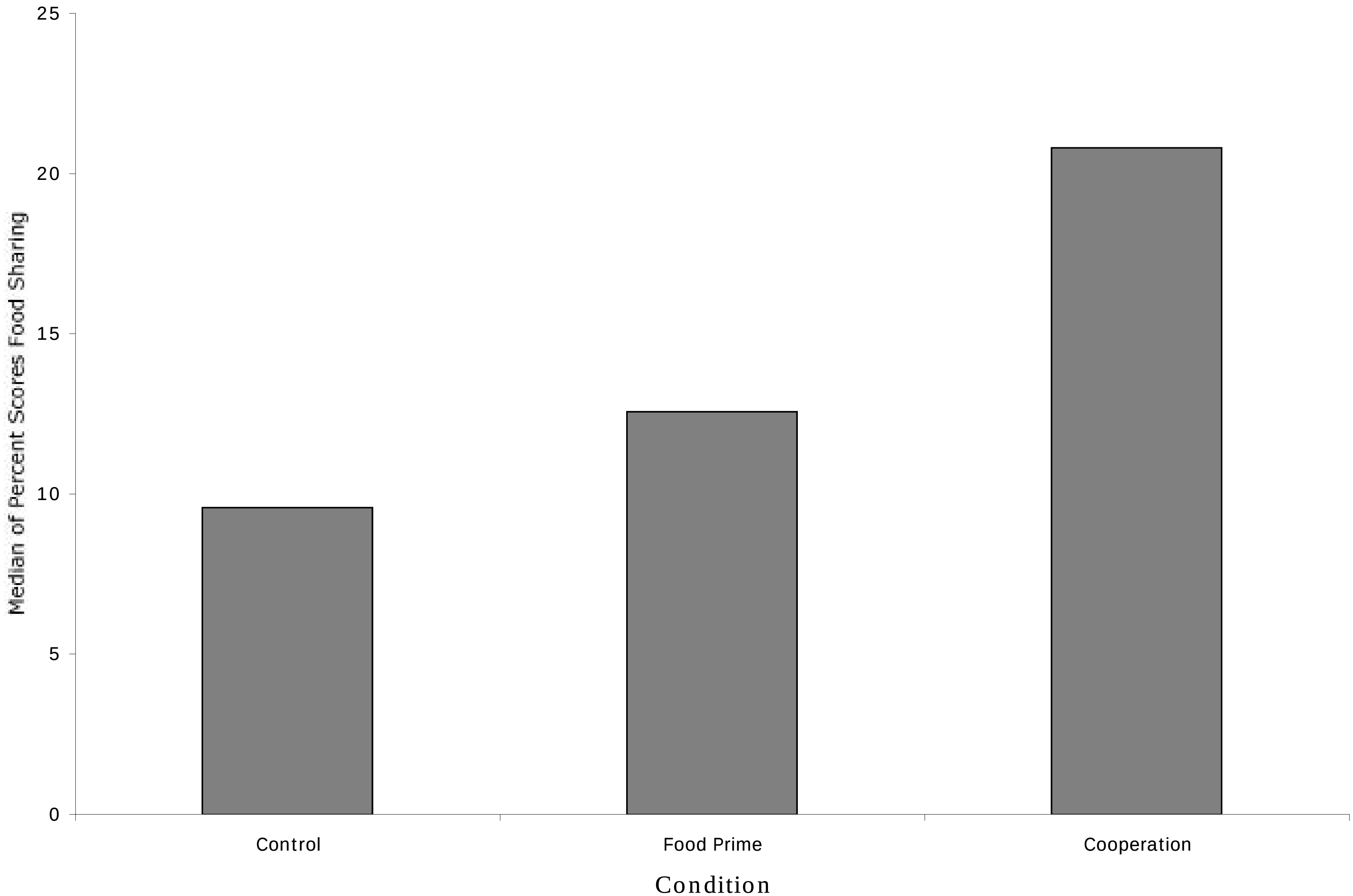
Figure 4. Median percentages of total time spent sharing food across the control condition from Experiment 1, the food prime condition from Experiment 2, and the cooperation condition from Experiment 1. Data from the same four subject pairs are presented.



Mean Percent of Total Time Food Sharing
40
35
30
25
20
15
10
5
0
Control
Cooperation
Caitlin/Dante
Fozzie/Zhivago
Ophelia/Olympia
Sebastian/Caitlin
Mac/Oprah
Rolo/Yohoo
Subject Pairs



25
20
15
10
5
0
Mean Percent of Total Time Food Sharing
First
Second
Order
Control
Cooperation



25
20
15
10
5
0
Median of Percent Scores Food Sharing
Control
Food Prime
Cooperation
Condition