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Food-related tolerance in capuchin monkeys (*Cebus apella*) varies with knowledge of the partner's previous food-consumption

Yuko Hattori [a,b,c,*], **Kristin Leimgruber** [c], **Kazuo Fujita** [a] and
Frans B.M. de Waal [c]

[a] Department of Psychology, Graduate School of Letters, Kyoto University,
Yoshida-honmachi, Sakyou-ku, Kyoto-shi, Kyoto, 606-8501, Japan
[b] Japan Society for the Promotion of Science, Asako Building, 5-3-1 Kojimachi,
Chiyoda-ku, Tokyo 102-0083, Japan
[c] Living Links, Yerkes National Primate Research Center, Emory University, 954 North
Gatewood Road, Atlanta, GA 30322, USA
[*]Corresponding author's e-mail address: yhattori@pri.kyoto-u.ac.jp

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Abstract

Capuchin monkeys, as well as several other primate species, show food-related tolerance in both captive and wild settings. Although researchers have revealed that past experience affects food-related tolerance, it is unclear if and how observing a partner's previous food consumption affects tolerance. This question is important to determine the proximate mechanism of food-related tolerance, which may lead to food sharing, co-feeding, or tolerated taking. We investigated whether perception of another's consumption of food affected the rate of tolerant food transfers among brown capuchin monkeys (*Cebus apella*). First, in the test condition, subjects observed their partner either eating (Eat–In View) or not eating food (No Eat–In View) through a window. In a control condition, the subjects could not observe the same partner behind an opaque screen, while the partner either ate (Eat–Out of View) or did not eat (No Eat–Out of View). After this, the subjects were provided with food to examine how well they tolerated their partner's access to it through the mesh. Tolerant food transfers were sharply reduced after the subjects had observed their partner eat, but not in the control condition or after they had observed the partner not eating. We consider two possible hypotheses for this behavior, one relates to the internal state of the subject after having seen their partner eat (i.e., increased competitiveness, aggression, or food motivation). The other hypothesis relates to how the subject understands the partner's motivational state after having witnessed food consumption, perhaps by grasping the partner's need.

Keywords

social cognition, altruism, food sharing, non-human primates, capuchin monkeys.

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1. Introduction

Sharing of resources is considered a crucial aspect of human evolution by researchers from diverse disciplines, including evolutionary biology, economics, and anthropology (e.g., Hamilton, 1964; Axelrod, 1984; Kaplan et al., 2000). In human development, sharing or giving are often seen as expressions of empathy. This may be related to, but is not the same as, theory-of-mind (ToM), because well before human children are capable of passing a critical false belief task, they not only respond to another's distress but also offer toys in order to console others (Rheingold et al., 1976; Zahn-Waxler et al., 1992). At around 18 months of age, the human infant begins to understand connections between the perceptions, desires, and needs of others (Wellman et al., 2000). Thus, empathetic perspective-taking ontogenetically precedes more advanced forms of ToM, which may also be true phylogenetically (de Waal, 2009).

On the other hand, although many nonhuman primates co-feed with conspecifics (e.g., prosimians (Gursky, 2000), New World monkeys (Brown & Mack, 1978; Perry & Rose, 1994; Kasper et al., 2008), Old World monkeys (Dittus, 1984) and chimpanzees (de Waal, 1989)), very few species, i.e., chimpanzees and some New World monkeys, such as capuchins, marmosets and tamarins, regularly share food outside the parent–offspring context. Most of their sharing is of a passive type, in which they allow others to feed on food that they are holding. Active donation of food does occur, but is relatively rare. In this study, we focus on tolerant food transfers also previously described as 'facilitated taking'. This is a situation where the food possessor and the partner are separated by a mesh partition and the food possessor allows the partner to take food through the mesh by sitting within reach of the partner (de Waal, 2000). 'Tolerant food transfer' is defined as all occasions on which the partner collected or received food either directly from the hands or mouth of the possessor or by picking up dropped food from within the possessor's reach and in full view of the possessor. This measure excludes quick or sneaky collections of food when the possessor had her back turned or sat at a distance from the partition. Thus defined, tolerant food transfers have been described as 'facilitated taking' since they depend on the possessor's willingness to transport food to within the other's reach and tolerate the other's taking of food (de Waal, 2000).

Recent studies demonstrate that food sharing, including tolerant food transfers, depend on the recent history of interaction with the partner. For example, if an adult chimpanzee, A, has groomed another adult, B, the tendency of B to subsequently share food with A is higher than if A has not previously groomed B (de Waal, 1997a). Another study has shown that capuchin monkeys share food more when they have recently cooperated with another individual to obtain this particular food (de Waal & Berger, 2000). In Callitrichids, who are known to actively give food (Burkart et al., 2007), it is also reported that reciprocity affects altruistic offering for food (Cronin et al., 2010).

According to these studies, some nonhuman primates change their food-sharing behavior with others flexibly depending upon past interactions. However, the experiential factors that cause this effect are hard to identify from previous studies because both individuals were likely affected at the same time. Here, we experimentally investigate if the subject's past visual experience with the partner eating food affects food-related tolerance. We hypothesized that this may occur either through knowledge of the other's hunger state, hence some form of perspective-taking, or a change in the observer's food-related motivation.

In our study, we looked at the behavior of a neotropical primate, the brown capuchin monkey (*Cebus apella*), which belongs to one of the very few primate genera in which unrelated adults spontaneously and often peacefully share food, both in the wild and in captivity (Perry & Rose, 1994; de Waal, 1997b). Specifically, we measured the effect of witnessing a partner's previous food consumption on subsequent tolerant food transfers to the same partner. Since any such effect could potentially be explained by differential food motivation in the partner and associated motivational changes (such as a greater interest in the subject's food), the experiment included control conditions in which the partner could either eat or not eat, but out of the subject's view. If tolerant food transfers were mainly induced by partner behavior, high rates of food transfer would be expected whenever the partner had not previously eaten regardless of visibility of this event or non-event to the subject. On the other hand, if tolerant food transfers depend on the subject's preceding observation of the partner eating food, we expect food transfers to be suppressed mainly if the subject had seen the partner eat beforehand.

2. Materials and methods

2.1. Subjects

The Yerkes colony consists of two separate social groups of brown capuchin monkeys. Each group includes 4 adult males and 8 or 7 adult females. The capuchin facility offers indoor/outdoor housing for the two groups with a total of 25 m^2 of floor space for one group, and 31 m^2 for the other. Normally, the monkeys have free access to their entire separate areas. Visual contact between groups was controlled by an opaque screen. The facility included a separate office with windows through which researchers could monitor the monkey area. The monkeys received ad libitum water and monkey chow, and a daily tray with bread, fruits and vegetables after the day's last test. All procedures were approved by Emory University's Institutional Animal Care and Use Committee (IACUC: 109-2005). The Yerkes National Primate Research Center is accredited by the American Association for Accreditation of Laboratory Animal Care. During the experiment, the monkeys were unrestrained and could move freely in the test chamber. They were returned to their group soon after the daily session.

Ten adult females participated in the experiment, and were always paired with an unrelated female partner of similar rank of her own social group on the basis of affiliative similarities. On different testing days, pairs were retested in reversed roles. We did not test males in order to exclude the behavioral influence of sex (de Waal, 2000). Because of small sample size, two monkeys participated twice, paired with different individuals, after a 6-month interval. Thus, our results contain data from 12 different pairs of monkeys. The subjects had been well trained for separation from their group. For testing, each pair was placed in an indoor test chamber, while the rest of the colony was kept outdoors. This allowed us to interact with the subjects in a controlled manner with minimal distractions. Dependent offspring were allowed into the testing area with their mothers.

2.2. Apparatus

A mobile test chamber of vinyl-coated mesh was attached to the front of a group's indoor pen. The test chamber was divided by inserting a mesh partition, providing each subject in a pair test with an area of 72 × 60 × 60 cm. Food bowls were attached to the outside of the chamber on either side, well out of reach of the monkey on the other side.

2.3. Conditions

Each session consisted of a 10-min Observation phase immediately followed by a 10-min Test phase. The monkeys were labeled the subject (the one given an opportunity to share in the Test phase) and her partner (the one whose eating behavior was manipulated in the Observation phase). In the Observation phase, one of the four conditions below was randomly chosen. These conditions (Figure 1) manipulated (a) the partner's food motivation in the Test phase (i.e., having eaten or not), and (b) the subject's experience of witnessing the partner's food consumption (i.e., partner visibility):

(1) Eat–In View: The partner ate food in full view of the subject.

(2) Eat–Out of View: The partner ate food behind an opaque partition, out of view of the subject.

(3) No Eat–In View: The partner had food in front of her but was prevented by a transparent Lexan panel from accessing while in full view of the subject.

(4) No Eat–Out of View: The partner had food in front of her but was prevented from accessing it behind an opaque partition, out of view of the subject.

In all of the Observation phases, the two monkeys were prevented from physical contact by a transparent or opaque Lexan panel dependent on the visibility condition. In out of view conditions, the subject could not see the food cup placed in front of the partner because of the opaque panel. The order of presentation of the conditions was randomized and counterbalanced across the 12 pairs. Each condition was conducted once per pair. The interval between Observation and Test phase was 1 min. No monkeys were tested more than once per day. A medium-sized apple cut into about 1 cm^3 pieces was given in both phases, which each monkey could monopolize unless she brought the food close to the mesh partition. All sessions were videotaped.

2.4. Dependent variables

In the Test phase, the subject was given food and the first author used videotapes to measure the rate of 'tolerant food transfers' as well as other food related interactions between the subject and the partner.

Additionally, we recorded the position of both subjects and partners every 30 s from videotapes relative to the partition by dividing each section of the test chamber into three equal parts (distance 1, close to the mesh partition;

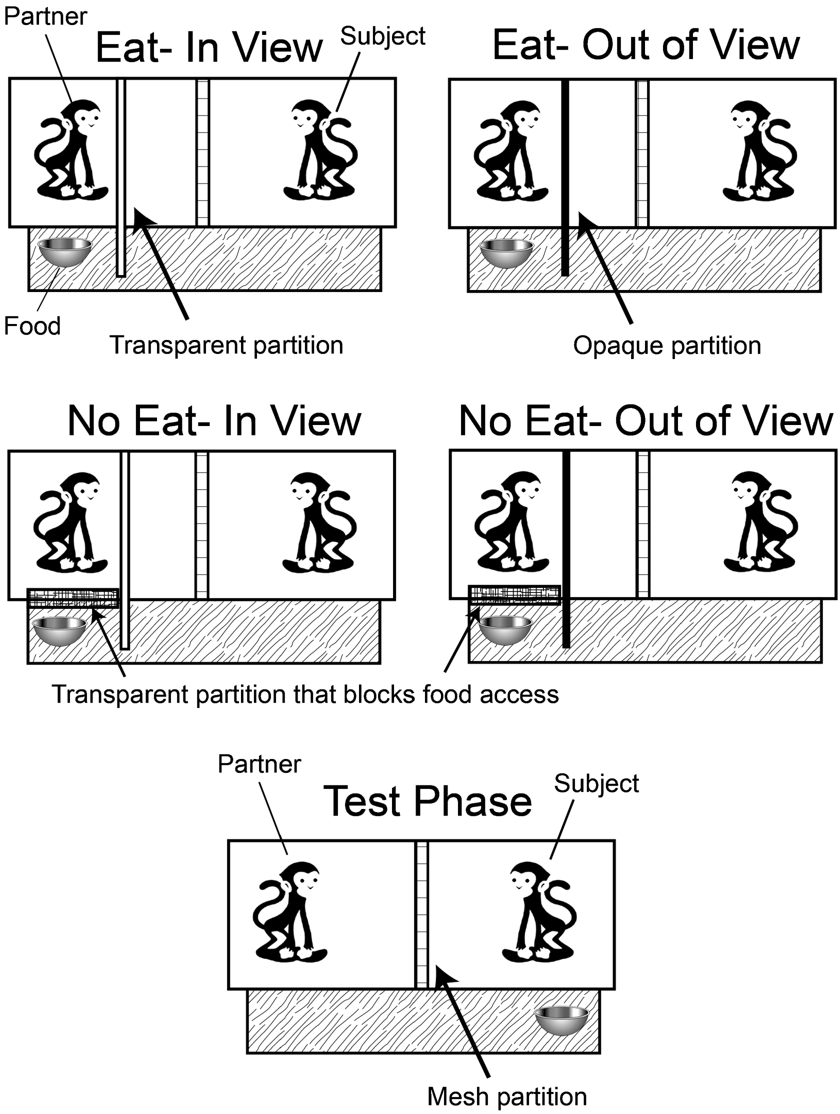

Figure 1. The 4 conditions of the 10-min Observation phase. (1) Eat–In View: the partner ate food in full view of the subject. (2) Eat–Out of View: the partner ate food behind an opaque partition. (3) No Eat–In View: the partner was prevented from accessing food while in view of the subject. (4) No Eat–Out of View: the partner was prevented from accessing food out of view of the subject. Test phase: the subject had access to food and was given a chance to share with the partner for 10 min.

distance 2, intermediate; distance 3, at the far end of the mesh partition) in order to test the hypothesis that food sharing might occur because the partner spent more time near the mesh when hungry. We measured the number of point samples (out of 20 per test) when the partner sat at each distance to the mesh partition. We also calculated the subject's food collection speed from the bowl to test the hypothesis that food sharing occurs depending upon the subject's motivation for food, which may hypothetically vary dependent on whether the subject had seen the partner eat or not eat. The food collection speed was defined in pieces taken from the bowl per minute during the 10-min Test phase. Finally, aggressive behavior by either monkey towards the other individual was also analyzed to see whether this behavior varied with the conditions. Aggressive behavior was defined as threatening the other individual through the mesh partition, banging the partition or aggressively vocalizing towards the other individual.

3. Results

For interobserver reliability on types of food related interactions between the subject and the partner, a second coder blind to the testing condition coded 12 sessions, 25% of all trials, from video. The Cohen's Kappa score of agreement with the first author was 0.772.

3.1. Tolerant food transfers

We used a Randomization test to statistically evaluate the effect of the partner's food motivation and the subject's experience with the partner's food consumption. In comparison with standard statistical methods, the Randomization Test has the advantage that it is non-parametric (i.e., does not require a normal distribution) and insensitive to data independence, because the same data points serve to evaluate the effect. Specifically, using one subject in two pairs poses no problem for this particular evaluation (Manly, 1997).

Figure 2 shows the mean frequency of tolerant food transfers during the test phase of the four conditions and Figure 3 shows data by subject. A Randomization Test based on 10 000 permutations revealed a significant difference in the frequency of 'tolerant food transfers' between In-view (Eat–In View: mean $=$ 2.25, SE $=$ 1.4) and Out-of-view (Eat–Out of View: mean $=$ 5.08, SE $=$ 2.78) conditions after the partner had eaten: there were fewer food transfers after the partner had eaten in view of the subject ($N = 12$,

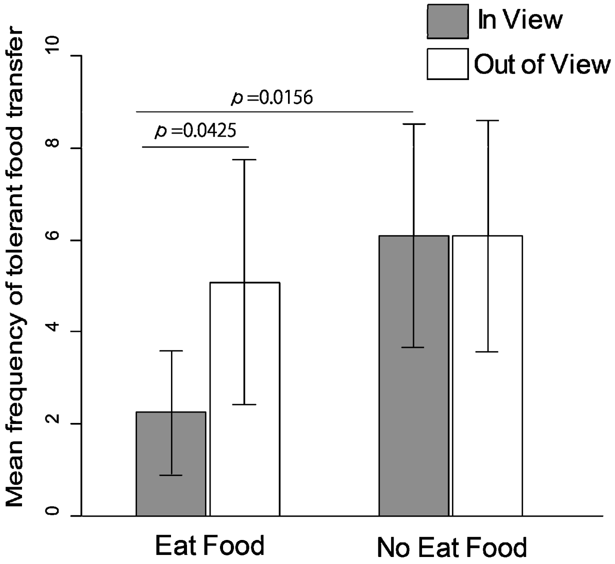

Figure 2. Mean frequency of tolerant food transfer during the Test phase (±SE).

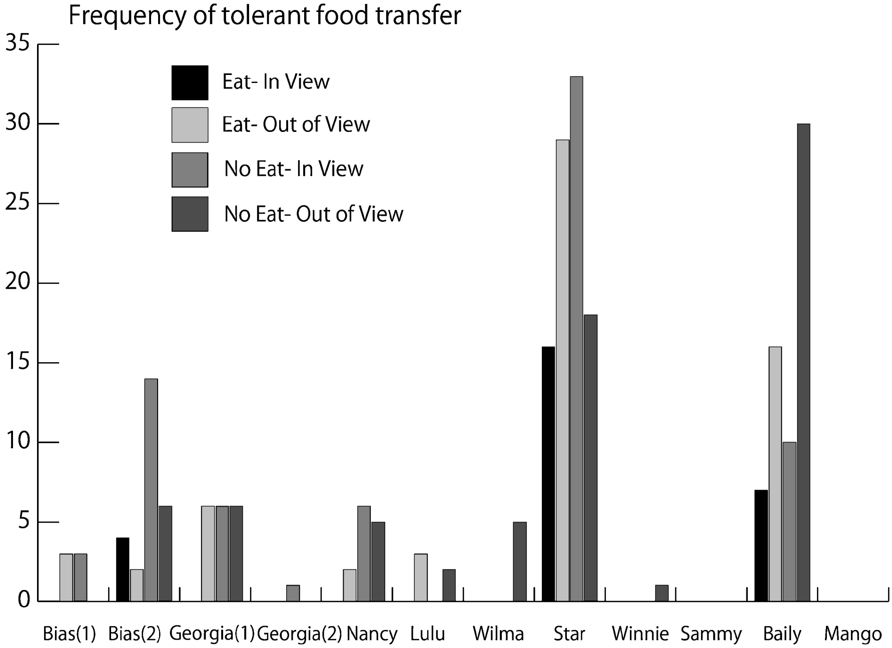

Figure 3. Individual data of frequency of tolerant food transfer during the Test phase.

$p = 0.0425$). The same difference was not observed between In-view (No Eat–In View: mean = 6.08, SE = 2.54) and Out-of-view conditions (No Eat–Out of View: mean = 6.08, SE = 2.62) when the partner had been unable to access food ($N = 12$, $p = 1$).

Comparing both In-view conditions (i.e., Eat–In View versus No Eat–In View), more food transfers occurred when the partner had not eaten ($N = 12$, $p = 0.0156$). Furthermore, the partner's motivation, as inferred from her having eaten or not, did not affect food transfers for both Out-of-view conditions ($N = 12$, $p = 0.5362$). Although large individual differences (e.g., tolerant food transfer did not occur in two monkeys) might suggest that several other factors other than previous visual experience also affect subsequent tolerant food sharing, overall there was a consistent tendency that tolerant food transfer was suppressed when the subject had seen the partner eating food.

3.2. Effect of order

In order to see if its previous role affected the subject, we analyzed the effect of order. If previous experience matters in tolerant food transfers, experiencing the role of partner in the past would lead to a higher rate of food transfer in the role of subject.

Because half of the monkeys took a role of 'Subject' first and the others took a role of 'Partner' first, we analyzed the effect of order of 'Subject' and 'Partner' roles, but found no significantly different frequency of tolerant food transfer between these groups ($N = 12$, $p = 0.621$). The mean frequency of tolerant food transfer by individuals who had acted as Subject first was 5.0 (SE = 3.5) and whereas for those who had acted as Partner first it was 4.75 (SE = 2.21).

3.3. Food collection by the partner out of the subject's view

In order to confirm that the different food transfers occurred only in the subject's view (i.e., 'tolerant food transfer'), we also analyzed 'other food transfer', defined as food collections by the partner that occurred outside the subjects' view.

Randomization Tests across the four conditions revealed no significant differences in any paired comparisons which we tested in 'tolerant food transfer' ($N = 12$, Eat–In View versus Eat–Out of View, $p = 0.353$; Eat–In View versus No Eat–In View, $p = 0.495$; Eat–Out of View versus No Eat–Out of View, $p = 0.760$, No Eat–In View versus No Eat–Out of View, $p = 0.784$).

3.4. Location relative to partition

In order to examine the locations of both partner and subject, we compared the conditions that showed a significant difference in food sharing (see above). If tolerant food transfers were induced by the proximity of partner or subject to the mesh partition, the same difference in tolerant food transfer would be revealed.

The same Randomization Test revealed no accompanying significant difference in partner or subject locations relative to the partition between Eat–In View and Eat–Out of View (partner: $N = 12$, $p = 0.569$; Eat–In View: mean score = 1.59, SE = 0.12; Eat–out of View: mean = 1.56, SE = 0.09; subject: $N = 12$, $p = 0.681$; Eat–In View: mean score = 2.55, SE = 0.13; Eat–Out of View: mean = 2.45, SE = 0.15). Also for Eat versus No Eat–In View (partner: mean = 1.53, SE = 0.12; subject: mean = 2.57, SE = 0.13), no significant difference was found (partner: $N = 12$, $p = 0.575$; subject: $N = 12$, $p = 0.389$) (Figure 4).

3.5. Food collection speed

We also analyzed food collection speed by the subject as a measure of food motivation, to determine if it changed as a result of having seen their partner eat.

The rate at which the subject collected food pieces from the bowl was measured from the videos. The food collection speed was defined in pieces taken from the bowl per minute during the 10 min Test phase. Overall, the subjects collected food faster in the first 5 min than in the second 5 min ($N = 12$, $p < 0.000001$, first 5 min: mean = 2.86, SE = 0.16, second 5 min: mean = 2.02, SE = 0.18). This indicates that food collection speed was influenced by the subjects' motivation for food because they were hungrier in the first 5 min than in the second 5 min. However, randomization tests found no significant difference in collection speed across conditions (Table 1).

3.6. Aggressive behavior

For both subject and partner, only a few monkeys showed aggressive behavior. For example, only one monkey showed aggressive behaviors in Eat–Out of View condition as subject and Eat–In View and Eat–Out of View conditions as partner. Two monkeys showed them in Eat–In View and No Eat–In View conditions as subject and No Eat–Out of View condition as Partner.

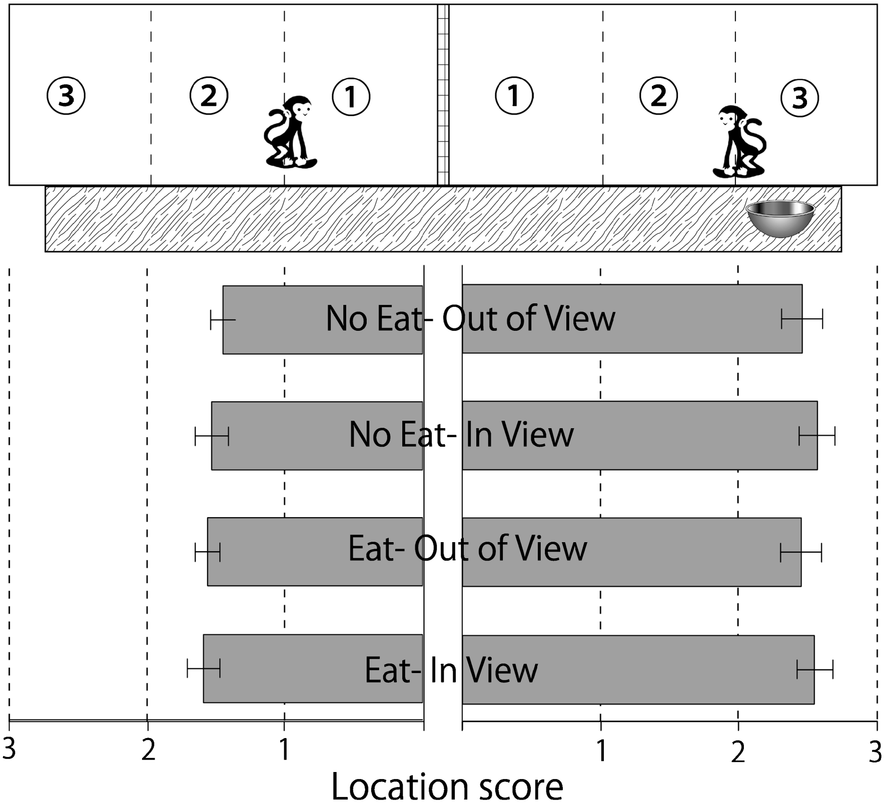

Figure 4. Mean location score relative to the mesh partition (1 is closest and 3 is most distant) of the subject and partner during the Test phase in four conditions (±SE).

Table 1.
Food collection speed by subject.

Subject ($N = 12$)	Eat–In View	Eat–Out of View	No Eat–In View	No Eat–Out of View
Eat–In View		$p = 0.532$	$p = 0.42$	$p = 0.632$
Eat–Out of View			$p = 0.742$	$p = 0.244$
No Eat–In View				$p = 0.289$
No Eat–Out of View				
Mean	1.2	1.28	1.25	1.15
SE	0.08	0.096	0.011	0.074

Table 2.
Frequency of aggressive behaviors by subject.

Subject ($N = 12$)	Eat–In View	Eat–Out of View	No Eat–In View	No Eat–Out of View
Eat–In View		$p = 0.495$	$p = 1.00$	$p = 0.375$
Eat–Out of View			$p = 0.502$	$p = 0.621$
No Eat–In View				$p = 1.00$
No Eat–Out of View				
Mean	0.25	1.87	2.67	1.17
SE	0.17	1.76	2.15	0.75

Table 3.
Frequency of aggressive behaviors by partner.

Partner ($N = 12$)	Eat–In View	Eat–Out of View	No Eat–In View	No Eat–Out of View
Eat–In View		$p = 0.375$	$p = 1.000$	$p = 1.000$
Eat–Out of View			$p = 0.252$	$p = 0.498$
No Eat–In View				$p = 1.000$
No Eat–Out of View				
Mean	0.083	0.67	1.17	0.17
SE	0.08	0.64	0.87	0.11

Three monkeys showed them in No Eat–In View condition as subject and in No Eat–Out of View condition as partner.

Mean frequency of aggressive behaviors by subject was 1.48 (SE = 1.18) and 0.52 (SE = 0.37) by partner. Again, randomization test revealed no significant differences in any paired comparison between conditions (Tables 2 and 3).

4. Discussion

The rate of tolerant food transfers dropped significantly if subjects had just seen their partner eat in the Eat–In View condition compared to other conditions in which subjects had either witnessed their partner without access to food or had not seen their partner either eat or not eat. Given that we manipulated the partner's previous food consumption as well as her visibility, these results are not easily explained by the partner's own food motivation. Furthermore, we found that the partner's proximity to the mesh partition did not vary across conditions. One would predict that higher food motivation would have caused closer proximity, but no significant differences in location were found. That the number of food transfers during the Test phase was under the subject's control was indicated by the fact that 'other food transfers', which fell outside the subject's control, did not show the same variation across conditions. Given that the subject and partner could not directly interact because of the mesh partition, the subject may have used visual cues such as monitoring and/or retrieving food to regulate the partner's access, as also suggested by earlier studies in this paradigm (de Waal, 1997b).

Importantly, our result suggests that when capuchin monkeys allow a partner to take from their food, they take past events into account. They seem to not just respond to the partner's current behavior, but also bring knowledge of the partner's state to the situation. To have such knowledge guide decisions about altruistic behavior should be beneficial for animals living in complex social groups. For example, it would be of great advantage for monkeys to limit food sharing to situations in which the other needs food, and to reduce it in situations in which the other is sated, hence to adjust sharing behavior based on the other's hunger state. This would represent a more efficient use of resources. Our data suggest that in fact monkeys make this adjustment based on observation of the partner's previous interactions with food.

At this moment, we suggest two possible mechanisms for a decreased frequency of tolerant food transfer after having seen the partner eat. The first is an internal one, which suggests that the food possessor's own motivation for food is modified by the partner's previous behavior, such as increased competitiveness or aggressive behaviors towards the partner or an increased food motivation leading to facilitated eating (i.e., motivational hypothesis). The second possibility is that food possessors change their attitude towards the partner based on an understanding of the partner's motivational state, or need, which is altered by its previous food consumption (i.e., other-oriented hypothesis). The data do not allow us to conclusively choose between both hypotheses, although evidence for the motivational hypothesis has some serious problems. For example, our data fail to show significant variation in the subject's own food motivation (as expressed in food collection speed) across the four conditions. In addition, the virtual absence of aggressive behaviors fails to support the motivational hypothesis' expectation of increased competitiveness or aggression after subjects had seen their partner eat.

This does not mean, however, that motivational hypothesis can be definitely excluded, because the interaction between both monkeys may be affected by motivational factors or behavioral changes that are not overtly expressed. One way to exclude this possibility in future research might be by manipulating the partner in the Observation phase and Test phase (e.g., by using a new partner in the Test phase).

The other-oriented hypothesis makes no predictions about the subject's food motivation or competition between both monkeys. It simply predicts that having seen a partner eat or not eat changes the perception of the partner's need, which perception will then affect the subject's preparedness to bring food to within the partner's proximity. Capuchin monkeys were more tolerant of partners taking food in their possession after having seen them not eating in the immediately preceding period. This may reflect perception of the other's need. Further experiments are needed to specify if capuchin monkeys truly possess this sensitivity, in accordance to the other-oriented hypothesis, which in human development is considered a cognitive precursor for empathic perspective-taking.

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