

BRIEF REPORT

Attending to the Outcome of Others: Disadvantageous Inequity Aversion in Male Capuchin Monkeys (*Cebus apella*)

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Brosnan and de Waal [Nature 425:297–299, 2003] reported that capuchin monkeys responded negatively to unequal reward distributions between themselves and another individual when comparing their own rewards with that of their partner. It was suggested that social emotions provided the underlying motivation for such behavior and that this inequity aversion is specific to the social domain. However, alternative hypotheses such as the “frustration effect” or the “food expectation hypothesis” may provide more parsimonious explanations for Brosnan and de Waal’s [Nature 425:297–299] results, while others have argued that these findings are not congruent with the Fehr–Schmidt inequity aversion model cited by the authors. The claim that inequity aversion behavior is specific to the social domain has also been questioned, as primates also develop expectations about rewards in the absence of partners, and react negatively when those expectations are violated. In this study, a modified Dictator game was used to investigate whether capuchins would exhibit either disadvantageous inequity aversion behavior or reference-dependent expectancy violation in social and nonsocial conditions, respectively. When given the choice between an equitable and an inequitable outcome, the subjects showed disadvantageous inequity aversion behavior, choosing the equitable outcome significantly more in the social condition. In the nonsocial condition, however, subjects did not show negative expectancy violation resulting from the formation of reference-dependent expectations, choosing the equitable outcome at chance levels. These results suggest that capuchins attend to differential payoffs and that they are averse to inequity, which is disadvantageous to themselves. Am. J. Primatol. 70:901–905, 2008. © 2008 Wiley-Liss, Inc.

Key words: disadvantageous inequity aversion; social cognition; capuchin

INTRODUCTION

Many studies demonstrate that humans show inequity aversion [Fehr & Fischbacher, 2003; Fehr & Schmidt, 1999], based on a comparison between the equilibrium of one’s own effort and reward, and the equilibrium of the effort and reward of the other person [Dubreuil et al., 2006]. A mismatch between these equilibria is perceived as unfair, either because it is advantageous or disadvantageous to the self. Brosnan and de Waal [2003] reported data supposedly demonstrating that capuchin monkeys are also inequity averse. However, this conclusion has not gone unchallenged.

Wynne [2004] pointed out that upon closer inspection Brosnan and de Waal’s interpretation based on inequity aversion is not well supported by their own data. In the “inequality test,” the monkeys refused to exchange a token for a nonpreferred food (cucumber) on 43% of trials when they saw a partner

receive a preferred food (grape) for the same effort. In the nonsocial “food control” condition, however, the same monkeys were just as likely to refuse the cucumber slice when they saw a grape placed where the absent partner normally sat (49% refusals). There can be no inequity when receiving a non-preferred food reward if nobody is receiving anything better. The mere presence of the better reward resulted in the monkeys refusing the nonpreferred reward.

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The high number of refusals when there was no partner along with the cognitive complexity of perceiving relations between relations opens the possibility of an alternative explanation for the findings of Brosnan and de Waal [2003]. Roma et al. [2006] suggested that the monkeys may have shown higher rejection rates owing to the well-known “frustration effect” that normally arises when subjects are initially given a high-quality reward followed by a low-quality reward. In other words, rejection is a consequence of the change in food quality rather than the difference between what the subject and the partner are receiving. Roma et al. [2006] provided empirical support for the frustration effect in a group of capuchins. However, in a recent study, van Wolkenten et al. [2007] ruled out this alternative explanation and showed that the capuchin monkeys’ negative responses to unequal reward distributions are affected by the sensitivity to individual energy expenditure or effort; they found that the lowest level of performance occurred when subjects were required to expend a large effort while at the same time seeing their partner receive a better reward.

Akin to the frustration effect, the food expectation hypothesis put forth by Bräuer et al. [2006] presents an alternative explanation, which suggests that the subjects’ (members from all of the great ape species) behavior is mainly determined by whether they expect to get the preferred food always visible to them. As in Dubreuil et al. [2006] and Roma et al. [2006], subjects did not have to exchange tokens for food. Bräuer et al. [2006] found that the apes ignored fewer pieces of the less-preferred food and stayed longer at the testing station when the conspecific got the favored food. Additionally, the subject begged more when the competitor was present than when s/he was not present. Taken together with Dubreuil et al.’s [2006] results, these findings contrast markedly with those of Brosnan and de Waal [2003].

Despite the current pursuit to determine the psychological underpinnings of inequity aversion in nonhuman primates, very little is known about capuchin monkeys’ sensitivity to inequitable outcomes. Current research has focused on their ability to recognize that rewards and efforts differ between individuals, and the resulting active avoidance of inequality disadvantageous to themselves. All a capuchin need do, if sensitive to inequity, is refuse to exchange the token for a lesser reward or simply refuse to accept the lesser food item from the experimenter. Brosnan and de Waal [2003] likened this behavior to that found in games designed to approximate the features of human bargaining. Directly relevant to their study is the “ultimatum game”; a one-trial game in which a “proposer” is given a sum of money to split between the proposer and another individual, known as the “responder.” The specified amounts are only paid to each

individual once the responder accepts the suggested distribution of money.

Although the connection between capuchin and human inequity aversion behaviors seems justified, there is a crucial difference between Brosnan and de Waal’s [2003] design and the ultimatum game—the responder’s rejection of the proposer’s distribution of funds creates income equity by assuring that neither is paid. Owing to the lack of this property in the design, the capuchin responders actually increased the inequity in the outcome by rejecting the cucumbers, because the conspecific continued to receive grapes. As Henrich [2004] noted, for there to be congruence of process between the results of the ultimatum game and the results reported by Brosnan and de Waal [2003], responders would have had to accept the cucumber offerings to reduce the inequity of the outcome between themselves and their models.

Given the precise processes within these economic games, the purpose of this study was to examine inequity aversion behavior within a modified Dictator’s game based on the properties of the Cardinal ultimatum game proposed by Bolton and Zwick [1995]. This consists of the standard ultimatum game, except that proposers have only two choices, an equitable allocation or a highly inequitable one. Capuchin subjects were given two choices, allowing them to select the context of their payoff; both choices led to the same payoff (one piece of food), but were framed as either equitable (conspecific received one piece of food) or inequitable (conspecific received three pieces of food). If sensitive to inequity, capuchins would be expected to choose the equitable option that delivered one piece of food to both the subject and the conspecific. In addition, a nonsocial condition in which the choices were the same but without the presence of a conspecific was given. If the capuchins reliably choose the equitable option in the social condition, then their choices in the nonsocial condition can help clarify what mediates inequity aversion behavior.

METHOD

Subjects and Housing

The subjects were eight adult male capuchin monkeys, (*Cebus apella*), ranging from 13 to 21 years of age. They were housed in pairs (MI and SO; LE and NI; CH and XE; JO and XV) in a single indoor room at the University of Georgia, with visual access to each other along with limited daily social interactions for enrichment. All had been reared with conspecifics, except JO, who was human-reared. They had ad libitum access to water and were not food deprived. All subjects had participated in various physical and social cognitive tests, but the procedure for this study was novel to them. The research was conducted in compliance with protocols approved by the University of Georgia’s Institutional

Animal Care and Use Committee, and the subjects were treated as stated in the American Society of Primatologists principles for the ethical treatment of nonhuman primates.

Apparatus

The apparatus was originally designed and implemented in a study on food-choice and food-giving in tufted capuchin monkeys [Takimoto et al., 2007]. It consisted of two plexiglass containers placed next to one another 4 cm apart on a rolling cart. Each container had an operator side and a recipient side (Fig. 1). The side with the drawer was the operator side. When pulled, the operator/subject was able to obtain the piece of food within. As the drawer was fully extended, a partition pushed food off a ledge and down a ramp so that the recipient could access the food through an opening. Each container was baited for both the operator (drawer) and the recipient (ledge). Only one drawer could be pulled at a time. As the recipient's side had no means to operate the drawer, the recipient was unable to control the operation of the apparatus.

Procedure

Before testing started all subjects were familiarized with the test apparatus both with a social partner and in the absence of a social partner. Additionally, at the beginning of testing, nonsocial knowledge probes were conducted to ensure that the capuchins were attending to the functioning of the apparatus. In these probes only one container was baited. When a subject met the criterion of choosing the baited drawer 80% of the time, it was deemed knowledgeable about how the apparatus functioned.

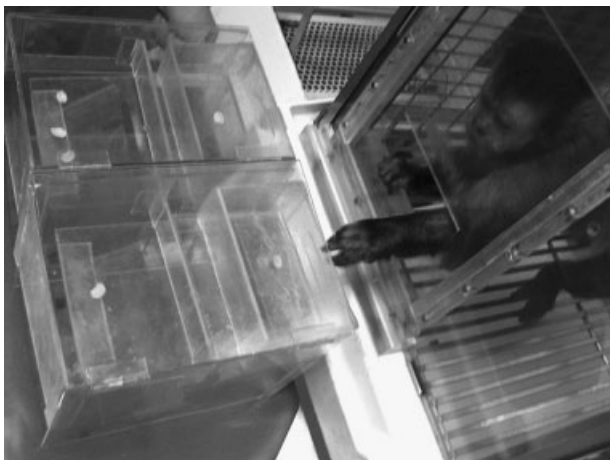


Fig. 1. Apparatus: top view of test apparatus. Subject is seen grabbing the drawer of the container of choice. By pulling, the subject will obtain the single piece of peanut within. Simultaneously, the single piece of peanut visible on either side of the container will be pushed off its ledge and ejected out the bottom of the container into within reaching distance of the conspecific partner sitting opposite (not seen).

Seven capuchins experienced both roles of operator and recipient. The eighth capuchin (JO) only acted as a recipient as he was unable to meet the criterion in the knowledge probes. Each operator was tested with the other seven capuchins acting as recipients, with order in which the monkeys acted as operators and recipients randomly assigned. Each operator was given a session which consisted of nonsocial condition trials both before and after the social condition session itself.

The food used throughout the experiment alternated between cereal, peanuts and craisins. Three food types were used to maintain subjects' interest and motivation in the task. The containers always contained the same food type; food type randomly changed when the subject was paired with a new partner.

Social Condition

In the social condition, the recipient could reach from its testing cage to obtain the food released from the container by the operator. The operator could only reach the food placed within the drawer of the container of its choice. Regardless of which container the operator chose, the payoff for the operator remained the same: one piece of food. However, based on the amount of food made available to the recipient, the framing of the payoff was different. If the operator chose the equitable container, both received one piece of food, whereas if the operator chose the inequitable container, the operator still received one piece of food, while the recipient received three. There were 12 social trials per session, with equitable and inequitable outcomes presented on the left and right sides equally frequently in counterbalanced order.

Nonsocial Condition

The nonsocial condition provided a direct comparison with the social condition. Both containers were baited in the same manner as in the social condition. However, the recipient was not present. Twelve nonsocial trials per session were run, six before the social condition and six trials after. The equitable and inequitable outcomes were presented on the left and right sides equally frequently in counterbalanced order.

RESULTS

All of the capuchins, with the exception of SO, exhibited varying degrees of inequity aversion behavior. A 2 (side) \times 2 (condition) repeated measures analysis of variance showed a main effect for the condition ($F_{1,6} = 5.687$, $\eta_p^2 = .487$, $P < .05$), with no main effect of side and no side \times condition interaction.

The average proportion of equitable choices made by each capuchin in both conditions is presented in Figure 2. In the nonsocial condition,

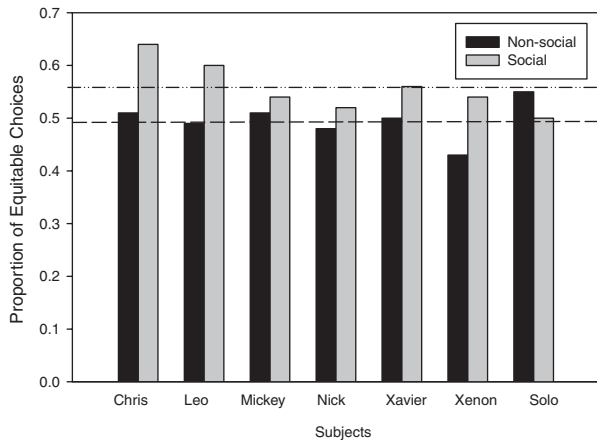


Fig. 2. Average proportion of equitable choices by individual capuchins in nonsocial and social conditions. Dashed and dotted lines represent the average proportion in the nonsocial and the social conditions, respectively.

the subjects did not choose the equitable option above chance $t(6) = -.366$, $P = .727$. If their inequity aversion behavior was based on a reference-dependent comparison (negative expectancy violation), the proportion of equitable choices made in this condition should have been reliably above chance. However, the proportion of equitable choices was reliably above chance in the social condition, $t(6) = 3.064$, $P = .022$. Additionally, a one-sample t -test indicated significantly more equity responses in the social than the nonsocial condition, $t(6) = 2.644$, $P = .038$.

As mentioned previously, subject SO did not exhibit inequity aversion behavior, but instead showed a decrease in equitable choices from the nonsocial condition to the social condition, contrasting with the other six capuchins. Although six out of the seven capuchins showed the expected direction of effect, only CH's pattern of results reached significance, $t(6) = 2.716$, $P = .008$. LE's data went in the same direction but failed to reach significance, $t(6) = 1.768$, $P = .081$. However, the remaining four capuchins' individual choices showed no statistically significant differences.

DISCUSSION

The data presented here suggest that capuchins may be adverse to inequity if this puts themselves at a disadvantage. Six of the seven subjects preferred an equitable outcome to an inequitable outcome and overall chose significantly more equitable outcomes in a social condition than in a nonsocial condition. Not only do these results suggest that capuchin monkeys are averse to disadvantageous inequity, they also highlight the importance of the social context in the expression of this behavior. Before accepting this conclusion, however, we need to consider three alternative hypotheses about inequity aversion behavior in nonhuman primates.

First, there is social facilitation, defined as an increase in the frequency of a behavior already in the animal's repertoire when in the presence of others engaged in the same behavior [Galloway et al., 2005]. Social facilitation would explain why subjects rejected less food in the social conditions in both Dubreuil et al. [2006] and Bräuer et al. [2006]. In this study, the focus was on the chooser and not the responder. As the operator's choice was the critical moment, the social facilitation hypothesis does not apply as an alternative explanation for the subjects' inequity aversion behavior.

Second, owing to the use of single food items in this study, the alternative explanation proposed by Roma et al. [2006] does not apply. The frustration hypothesis can be ruled out because subjects could only ever obtain a single food item; inequity was created by quantitative, not qualitative variation in available food. Third, the food expectation hypothesis [Bräuer et al., 2006] postulates that subjects expect to receive a preferred food in some conditions but not in others. However, this criticism can be ruled out here because subjects were always given the same food.

Although Brosnan and de Waal's [2003] findings have been criticized on theoretical grounds, grounds that this study has aimed to remove, another interesting difference emerges. Those authors reported inequity aversion behaviors only in female capuchin monkeys, claiming that only females reacted differently to conditions of "equality" and "inequality"; because males were not less willing to exchange for a less-favored food they were dropped from the study. Subsequent studies on inequity aversion in capuchins [Dubreuil et al., 2006; Roma et al., 2006] have also used only females, so very little is known about male sensitivity to inequity. Although a conclusive comparison of the sexes has yet to be done, the present finding of inequity aversion behaviors in male capuchins brings the existence of a sex difference into question; in any case further experimental evidence is needed to address differences in sensitivity to inequity by nonhuman primates.

Despite important differences between the designs of this study and others, the importance of the social context in inducing inequity aversion behavior is clear. Even though research has shown that both humans and nonhuman primates develop expectations about rewards in nonsocial settings and react negatively when those expectations are violated, the exhibition of inequity aversion is clearly influenced by the presence of a conspecific. If inequity aversion was predicated on the formation and violation of reference-dependent expectations regardless of context, the capuchins should have chosen the equitable outcome in the nonsocial condition more than would be expected by chance alone. However, in this study, subjects chose the

equitable outcome significantly more in the social condition than in the nonsocial condition.

In conclusion, the present results suggest that capuchin monkeys attend to differential reward distributions and exhibit disadvantageous inequity aversion behavior. As highly social animals with well-developed food sharing and cooperation [de Waal, 1997; de Waal & Davis, 2003; Mendres & de Waal, 2000], capuchins may hold socially mediated expectations about reward distribution and exchange that lead them to be averse to disadvantageous inequity.

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