ANIMAL BEHAVIOUR, 2007, 74, 487–496
doi:10.1016/j.anbehav.2007.01.015

Effects of food preferences on token exchange and behavioural responses to inequality in tufted capuchin monkeys, *Cebus apella*

M. B. FONTENOT*, S. L. WATSON†, K. A. ROBERTS* & R. W. MILLER*
*University of Louisiana at Lafayette-New Iberia Research Center
†University of Southern Mississippi

(Received 10 March 2006; initial acceptance 29 April 2006; final acceptance 15 January 2007; published online 23 August 2007; MS. number: A10387)

We examined the extent to which female capuchin monkeys show an 'aversion to inequitable work effort' by providing the monkeys with the opportunity to engage in token exchange tasks to earn either a preferred (grape) or nonpreferred (oat cereal) food item. In experiment 1, monkeys were paired with partners such that both were required to exchange a token (work effort) for either a preferred or nonpreferred food reward. The subject's exchange behaviour was then compared to conditions in which the partner received the food reward for no work effort. We found no evidence that differential work effort influenced the percentage of incomplete exchanges. Furthermore, capuchins completed exchanges more rapidly for the preferred food item, regardless of the work effort of the partner. In experiment 2, we evaluated, in the absence of differential work effort, behavioural responses of monkeys to receipt of a preferred or nonpreferred food in conditions where their partner received either the same or different food. These conditions were compared to control conditions where either the same or different food was placed in an adjacent empty cage. Capuchins were less likely to accept nonpreferred food and consumed it more slowly than preferred food. We found no evidence that the presence of a partner influenced acceptance or consumption of the nonpreferred food under inequitable conditions. Overall, we found no indication that capuchins are able to evaluate either the relative work effort of a partner or the inequity of a food reward and are thus unlikely to possess an 'aversion to inequity'.

Keywords: *Cebus apella*; exchange behaviour; food preference; inequality; token exchange; tufted capuchin

Many species of nonhuman primates have complex social systems and, consequently, engage in complex social interactions with conspecifics. Examination of such social complexities may afford an opportunity to make inferences about shared evolutionary origins with some human behaviours. Fehr & Schmidt (1999) suggested that human beings are averse to social inequities, which may be a necessary component (e.g. cheater detection) of the evolution of cooperation among human beings (Fehr & Fischbacher 2003). Thus, a 'sense of fairness' (Brosnan & de Waal 2003, page 297) may be a universal characteristic of human beings that is shared, in some form, by other highly social primate species.

Brown capuchins, *Cebus apella*, are known to be highly cooperative and have been used to study intraspecific social interactions, believed shared (at least to some extent) with humans. Building on previous observations that capuchins will readily exchange objects (i.e. tokens) for preferred food items (Westergaard et al. 1998, 2004) and will, in some cases, coordinate (work) efforts with conspecifics to procure preferred foods (Mendres & de Waal 2000; de Waal & Davis 2003). Brosnan & de Waal (2003) attempted to examine whether capuchins were able to understand second-order relations in token exchange. Specifically, they suggested that capuchins were able to evaluate differential value of food rewards received by another relative to their own reward. This effect was only partially tested because their subjects always received the nonpreferred food. They further

Correspondence: M. B. Fontenot, UL Lafayette-New Iberia Research Center, 4401 W. Admiral Doyle Dr., New Iberia, LA 70560, U.S.A. (email: bfontenot@louisiana.edu). S. L. Watson is at the University of Southern Mississippi, 118 College Dr., Box 5025, Hattiesburg, MS 39406, U.S.A.

0003–3472/07/$30.00/0

concluded that their capuchins evaluated differential effort expended by conspecifics for given rewards relative to the subjects' own effort. However, given the absence of an experimental condition in which reward inequity could be evaluated independently of work effort, this effect was not tested. Finally, they conclude that their capuchins evaluated the equity of their own work–food reward relation compared to the work–food reward relation of the conspecific partner. This effect, as well, was only partially tested. Thus, the authors understood but did not adequately test the necessary precursors to an understanding of second-order relation inequity.

Brosnan & de Waal (2003) employed four experimental conditions: an Equality condition, where each capuchin exchanged a token with an experimenter for a nonpreferred food item (i.e. cucumber; equal effort, equal reward); an Inequality condition, where the partner exchanged a token for a grape (preferred item) and the subject exchanged a token for a cucumber (nonpreferred food item; equal effort, unequal reward); an Effort control condition, where the partner received a grape for free while the subject exchanged a token for a cucumber (unequal effort, unequal reward); and a Food control condition, where a grape was placed in an empty cage visible to the monkey while the subject exchanged a token for a cucumber (unequal reward control). The exchange tendency varied across all four conditions and the presence of a preferred food reduced the tendency to exchange for a nonpreferred food. Furthermore, the tendency to exchange was influenced by the difference in effort between partners. It was concluded that capuchins 'measure rewards in relative terms, comparing their own rewards with those available, and their own efforts with those of others' (Brosnan & de Waal 2003, page 299). They concluded further that capuchins 'respond negatively to unequal reward distribution in exchanges with a human experimenter' (Brosnan & de Waal 2003, page 297) when the monkeys witnessed their experimental partner gain a more attractive reward for equal effort. The implications of Brosnan & de Waal's (2003) study suggest that the behaviour of these capuchins may represent an evolutionary forerunner to a human 'sense of fairness'.

An alternative explanation for Brosnan & de Waal's (2003) findings, given that they found no differences in mean frequency of exchange behaviour between their inequity and food control conditions, is that refusal to complete exchanges may reflect a tendency to reject a low-value reward simply because a higher-value reward is present (Wynne 2004). Upon reanalysis of their data, Brosnan & de Waal (2004) found that frequency of refusals to exchange decreased over time in the food control condition and increased over time in the inequity and effort control conditions, suggesting that capuchins were able to differentiate conditions in which a conspecific consumed a more preferred food from the mere presence of the preferred food.

Others suggest that the capuchins failed to exchange tokens for the less preferred food because they may have expected to receive the more preferred food. The expectation may have been elicited by the mere presence of the preferred food (Dubreuil et al. 2006) or by previous receipt of the more preferred food on earlier trials (Roma et al. 2006). Thus, the capuchins may have shown 'frustration' when presented with the less preferred food (Tinklepaugh 1928; Amsel & Roussel 1952). Roma et al. (2006) and Dubreuil et al. (2006) eliminated the work effort/food inequity confound in their studies by eliminating token exchange from their designs. Roma et al. (2006) found that capuchins were more likely to reject the less preferred food if they had previously been offered the more preferred food compared to rejection rates of those who had only received the less preferred food, supporting the 'frustration' hypothesis (see also Brosnan & de Waal 2006). Dubreuil et al. (2006) found that capuchins refused a less preferred food more often when a more preferred food was visible in the absence of a conspecific. Presence of a conspecific consuming a preferred food did not alter capuchins' acceptance of the less preferred food. Neither of these studies directly challenges the interpretation of Brosnan & de Waal (2003) nor did either attempt to address the question of whether capuchins are able to make second-order value assessments with respect to work effort of a conspecific.

Here, we report the results of two experiments in which we examined capuchin response to partner work effort inequity and reward value inequity, respectively. In experiment 1, we used an alternative design that extends that of Brosnan & de Waal (2003) to investigate whether capuchin monkeys evaluate the work effort of others relative to their own in the absence of food inequity. In experiment 1, animals were required to exchange a token for food while the partner either exchanged a token or received the same food for no effort. If capuchins possess an aversion to work inequity, we hypothesized that they would have higher rates of incomplete exchanges and/or increased latency to exchange a token, demonstrating an unwillingness to cooperate in conditions where their partner received the reward without effort. In experiment 2, we examined behavioural responses to food inequity (differential food quality disbursement) and food preference while holding work effort constant. If capuchins are averse to food value inequity, we hypothesized that capuchins would be less likely to accept and/or consume a food reward and may display increased aggressive or escape behaviour only in conditions in which a different reward is offered to its partner. Alternatively, if food preferences underlie behavioural responses, we would expect that capuchins would be less likely to accept and/or consume a food reward and may display increased aggressive or escape behaviours in all conditions in which the subjects receive the less preferred food in the presence of more preferred food, regardless of the presence of the partner. Prior to each experiment we determined the relative social rank of each individual, allowing us to control for potential variance due to dominance status.

METHODS

Subjects

The subjects were five laboratory-bred female capuchins, *Cebus apella*, aged 3.5 to 21 years at the start of