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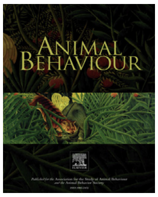

Capuchin monkeys, *Cebus apella*, show no evidence for inequity aversion in a costly choice task

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Human adults and children respond negatively to inequity, even sacrificing personal gain to avoid both disadvantageous (more for you, less for me) and advantageous (more for me, less for you) resource allocations. Recent work has argued that some nonhuman animals share this response, but findings for inequity aversion outside of humans are controversial. Unfortunately, animals' negative responses to inequity are difficult to interpret because animal inequity aversion tasks differ in critical ways from the tasks used to test human inequity aversion. Here we present evidence from a novel task testing disadvantageous and advantageous inequity aversion in capuchin monkeys, *Cebus apella*. Our task was designed to closely mirror inequity aversion studies of human adults and children. We found no evidence for either disadvantageous or advantageous inequity aversion. Instead, capuchins' decisions were guided solely by the food resource that they were offered. Moreover, subjects' decisions and reaction times did not vary across social and nonsocial conditions. Our findings suggest that capuchin monkeys do not exhibit a human-like response to inequity on tasks in which even young children are known to demonstrate inequity aversion. We discuss these results in the context of existing theories for the evolution of fairness.

A large body of evidence from laboratory and field experiments has revealed that human adults respond negatively to unfair resource distributions. People across societies reject payoff distributions that put them at a disadvantage relative to a peer ('disadvantageous inequity aversion'; Dawes, Fowler, Johnson, McElreath, & Smirnov, 2007; Fehr & Schmidt, 1999; Henrich et al., 2005; Güth, Schmittberger, & Schwarze, 1982) and, perhaps more surprisingly, will in some cases reject payoff distributions that put them at an advantage relative to a peer ('advantageous inequity aversion'; Dawes et al., 2007; Fehr & Schmidt, 1999). Additionally, this aversive response to unequal resource distributions appears to have deep roots in human development. Recent work on children in Western societies has shown that young infants are surprised when they see resources divided unequally between two individuals (Geraci & Surian, 2011; Schmidt & Sommerville, 2011; Sloane, Baillargeon, & Premack, 2012). Moreover, Western children show a growing concern for equality as they age (Benenson, Pascoe, & Radmore, 2007; Blake & Rand, 2010) and, by the age of 4 years, show a willingness to sacrifice their own rewards to prevent a disadvantageously unequal distribution (Blake & McAuliffe, 2011). Later, around 8 years of age, children will also sacrifice rewards to avoid advantageous distributions (Blake & McAuliffe, 2011; Shaw & Olson, 2012). Taken together, these findings suggest that an aversion to inequity develops early, is likely ubiquitous in our species and leads to costly decisions.

Fairness concerns are thought to play a role in stabilizing cooperative interactions in human societies (Fehr & Schmidt, 1999): individuals may benefit from tracking contributions to, and rewards from, cooperation and avoiding situations in which rewards are distributed unfairly with regards to investment. Moreover, a negative response to unfair reward distributions may motivate people to punish selfish individuals (Raihani & McAuliffe, 2012), thereby promoting future cooperation. Given the potentially important role that fairness concerns play in human cooperation, it is possible that other cooperative species are sensitive to inequity as

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well. Understanding whether and to what extent nonhuman species share the human-like response to unfair resource distributions could shed light on the selective forces that shaped this response in humans (Brosnan, 2006, 2011; Chen & Santos, 2006).

A number of studies have tested whether nonhuman species show an aversion to unfair resource distributions, and the findings to date have been equivocal (Bräuer & Hanus, 2012; Brosnan, 2011). Evidence for inequity aversion comes from studies of a number of species, including capuchin monkeys, *Cebus apella* (Brosnan & de Waal, 2003; van Wolkenten, Brosnan, & de Waal, 2007), domestic dogs, *Canis familiaris* (Range et al., 2009), chimpanzees, *Pan troglodytes* (Brosnan, Schiff, & de Waal, 2005), and rhesus macaques, *Macaca mulatta* (Massen, van den Berg, Spruijt, & Sterck, 2012). These studies have employed variations on an experimental paradigm in which a subject and recipient perform an action (e.g. trading a token) in order to secure a food reward. In 'equality conditions', an experimenter pays both individuals equally for performing the action. In 'inequality conditions', one individual is paid less for the same task: the subject watches his partner work for a high-quality reward and then the experimenter asks the subject to work for a poor-quality reward. Findings from such studies (e.g. Brosnan & de Waal, 2003) have revealed that some individuals refuse to perform the task when they have been given a disadvantageous payoff. Such results have been interpreted as evidence for a nonhuman analogue or homologue of humans' aversion to inequity (Brosnan, 2006, 2011; Brosnan & de Waal, 2003; Range et al., 2009; van Wolkenten et al., 2007). While these results hint at the possibility that other species share a human-like response to inequity, they are controversial for two reasons. First, several attempts to replicate some of these findings have been unsuccessful (Bräuer, Call, & Tomasello, 2006, 2009; Roma, Silberberg, Ruggiero, & Suomi, 2006; Silberberg, Crescimbene, Addessi, Anderson, & Visalberghi, 2009). Second, researchers have argued that these effects can be explained by alternatives other than an aversion to inequality. Specifically, several researchers have examined whether subjects reject unequal allocations because they are frustrated at not being able to access the more desirable reward (e.g. Bräuer et al., 2006; Bräuer et al., 2009; Hopper, Lambeth, Schapiro, & Brosnan, 2014; Roma et al., 2006; Silberberg et al., 2009). In Brosnan and de Waal's (2003) study, subjects were as likely to reject inequality when the better reward was delivered to the adjacent cage as when it was delivered to a conspecific, suggesting that they may have been frustrated at not being able to secure the better reward. Dubreuil, Gentile, and Visalberghi (2006) tested this alternative account by presenting capuchins with a less preferred food when a preferred food was present and found that the presence of the preferred food was sufficient to produce rejections of the less preferred food. These results lend support to the interpretation that frustration rather than inequity aversion produced the behaviour seen in Brosnan and de Waal (2003). While this result suggests that frustration may be an important driver of decision making, work on rhesus macaques suggests that it does not drive all decisions in such social tasks. Using a reward donation task, Chang, Winecoff, and Platt (2011) showed that rhesus monkeys prefer to donate food to a conspecific rather than to an empty chair, suggesting that subjects were not generally frustrated when they could not access rewards. More evidence against the frustration account comes from a recent study testing whether frustration explains chimpanzees' rejections of inequity (Hopper et al., 2014). In that study, researchers presented chimpanzees with an 'individual contrast' condition in which subjects were shown a more preferred food and then offered a less preferred food. They then compared responses in this condition to responses in an inequity condition ('social contrast') in which the partner but not the subject received the more desirable food. Hopper et al. (2014) found that inequity aversion and not frustration motivates rejections in chimpanzees, but similar tests that compare these conditions directly have yet to be conducted with other species. As such, frustration may still account for apparent inequity aversion in other animal species.

Inconsistencies in results from animal inequity aversion are difficult to reconcile with robustness and ubiquity of evidence for human inequity aversion. One possible explanation for why animal inequity aversion results do not clearly align with results from human studies is that the tasks used to test different species vary in critical ways. Namely, in the types of tasks used to test inequity aversion in humans (e.g. the Ultimatum Game in adults and children: Güth et al., 1982; Sutter, 2007; Inequity Game in children: Blake & McAuliffe, 2011), rejections of inequity promote equality because neither player gets anything. This is in striking contrast to animal inequity aversion tasks in which the act of refusing low-quality rewards increases the inequity between subjects and their partners (Henrich, 2004). Consider the case of Brosnan and de Waal's (2003) task with capuchin monkeys. In this task, two capuchin monkeys traded tokens with an experimenter. In the 'equal' condition they were paid equally for trading: they both received a piece of cucumber, a low-value food item. In the 'inequity' condition, the subject watched his or her partner trade for a grape, a high-value food item, and was then given an opportunity to trade for a piece of cucumber. Results from this study showed that subjects were more likely to refuse trading opportunities in the inequity condition than in the equal condition. However, refusals in this task increased rather than decreased the inequality between subject and partner (Henrich, 2004). This means that rejections in this task could not serve the purpose of reducing inequity but, instead, may have been a signal of frustration. Highlighting the importance of this issue, McAuliffe, Blake, and Warneken (in press) showed that young children are much more likely to reject inequity when doing so eliminates inequality than when doing so increases inequality as it does in animal tasks. Unfortunately, most animal experiments to date involve tasks in which subjects can signal their frustration and intolerance of unequal pay by rejection of unfair allocations, but their rejections have no material effect on their partners' payoffs. Thus, it is possible that animals may show more consistent inequity aversion in a task that more closely mirrors inequity aversion tasks in humans.

In this study we attempt to reconcile the findings from animal and human inequity aversion studies by testing a nonhuman animal on an inequity aversion task that can be directly compared to human inequity aversion tasks. We designed our task to be conducted with capuchin monkeys because this species has previously been identified as a likely candidate for inequity aversion (see Brosnan, 2011). Moreover, multiple studies have previously examined capuchin monkeys' responses to unequal reward distributions in a variety of tasks (Brosnan & de Waal, 2003; Dindo & de Waal, 2007; Fletcher, 2008; Roma et al., 2006; Silberberg et al., 2009; van Wolkenten et al., 2007) but the question of whether or not capuchins are indeed inequity averse is still open (Bräuer & Hanus, 2012; Sheskin, Ashayeri, Skerry, & Santos, 2013).

In the current study, we designed a novel nonhuman inequity aversion task that closely mirrors a method used to study inequity aversion in children (Blake & McAuliffe, 2011; McAuliffe, Blake, Kim, Wrangham, & Warneken, 2013; McAuliffe et al., 2015). In this task, an experimenter allocated resources between two individual capuchins, an actor and a recipient. The resources were either allocated equally or unequally. The actor was then given the opportunity to accept or reject a given allocation. If the actor accepted, she enacted the distribution of resources between herself and her partner. If she rejected the given allocation, she prevented the resources from being distributed. The critical feature of this design in comparison to past work on inequity aversion in animals is that rejections reduced inequity by affecting the payoffs of both the actor and the recipient.

Our novel task design allowed us to test whether capuchin monkeys' were willing to pay a cost to avoid both disadvantageous and advantageous inequity. As discussed above, several studies have tested animals in disadvantageous inequity conditions, but relatively few have tested whether animals respond to advantageous inequity. The few studies that have tested animals' reactions to advantageous inequity aversion (Brosnan, Talbot, Ahlgren, Lambeth, & Schapiro, 2010; Horowitz, 2012; Sheskin et al., 2013) have not done so in a costly choice task. In noncostly choice tasks, animals have shown weak evidence (Brosnan et al., 2010) or no evidence (Horowitz, 2012; Sheskin et al., 2013) for advantageous inequity aversion. However, just as typical disadvantageous inequity tasks differ from human tasks in important ways, so do the advantageous inequity tasks. Thus, to truly understand the limits on animals' responses to advantageous inequity it is important to test nonhumans in a task that is equivalent to the costly choice tasks used with human adults and children (Blake & McAuliffe, 2011; Dawes et al., 2007).

To measure subjects' responses to inequity, we used two dependent measures of capuchin behaviour. First, we examined subjects' propensity to accept versus reject reward allocations that were either equal or unequal (‘rejection rates’). We expected individuals to reject more frequently when faced with inequitable allocations than when faced with equal allocations. Second, we measured the time it took subjects to make a decision (‘reaction time’). Reaction time measurements have been used in the past to gain insight into subjects' decision making (Blake & McAuliffe, 2011; Piovesan & Wengström, 2009; Raihani, McAuliffe, Brosnan, & Bshary, 2012; Rand, Greene, & Nowak, 2012). In our task, we expected reaction times to reflect subjects' motivation to accept food allocations. If subjects show an aversion to inequity, they should be less motivated to accept, and thus react more slowly. Slow reaction times may also reflect conflict in subjects' decision making.

METHODS

Subjects

Subjects were eight brown capuchin monkeys, all of which were born in captivity and raised in a single social group as members of the capuchin colony at the Comparative Cognition Laboratory at Yale University (see Supplementary Table S1 for subject information). All members of the colony were communally housed in a large enclosure divided into five freely accessible sections. Subjects were fed monkey chow twice per day, once in the morning and once in the evening, as well as treats such as fruits, vegetables, nuts and cereal. Subjects had continual access to water in their home enclosures and during testing.

Subjects were assigned to the roles of ‘actor’ or ‘recipient’ (a.k.a. stooge). Actors consisted of one male and five females and recipients consisted of one male and one female. Actors were chosen based on their stable preferences for the two food items used in testing (see below). Actors ranged in age from 4 years old to 17 years old and ranged in social status from low ranking to high ranking (based on informal social observations). Recipients were the two lowest-ranked individuals in the colony; these individuals were selected based on prior experience as stooges as well as their low rank, which served to control for potential rank effects. Specifically, actors might be less willing to deny food to higher-ranking individual. Actors and recipients never swapped positions. All subjects had previously participated in a number of cognitive tasks, including studies on prosocial preferences and inequity aversion (see Supplementary Table S1; Lakshminarayanan & Santos, 2008; Sheskin et al., 2013; Skerry, Sheskin, & Santos, 2011).

Design

Experimental data were collected between July 2012 and July 2013. Each actor participated in two conditions: ‘advantageous inequity’ and ‘disadvantageous inequity’ (see Supplementary Fig. S1 for an illustration of our study design). The order in which the advantageous and disadvantageous conditions were conducted was counterbalanced between subjects. Each actor was paired with one recipient monkey for the advantageous inequity condition and with the other recipient for the disadvantageous inequity condition. Recipient pairings were counterbalanced between subjects. Prior to testing, preference tests were conducted to ensure that all actors showed a strong preference for the high-value food item (Kix, a breakfast cereal) over the low-value food item (Rice Krispies, also a breakfast cereal).

Within conditions, actors were tested in 10 sessions, which were run on separate days. These 10 sessions were divided into five ‘social’ sessions, in which actors were tested with a recipient, and five ‘nonsocial sessions’, in which actors were tested alone. In nonsocial sessions a stooge was present but was not given access to the recipient's chamber. We ensured that the recipient was present to hold potential distraction effects constant between social and nonsocial sessions. Session type (social versus nonsocial) was randomized within condition.

Each session consisted of 25 trials, five trials of each of the five treatments. Trial type was randomized within session. The five treatments were divided into three equality treatments and two inequality treatments (Table 1).

The equality treatments were identical across disadvantageous and advantageous conditions and were as follows: (1) high equity, in which both actor and recipient could receive one high-value food item; (2) low equity, in which both actor and recipient could receive one low-value food item; (3) nothing equity, in which both actor and recipient could receive one nonfood item (a peanut shell). The nothing equity treatment was designed to tests actors' baseline levels of rejection.

The inequality treatments varied across disadvantageous and advantageous conditions. In the disadvantageous condition, inequity treatments were as follows: (1) quality inequity, in which the actor could receive one low-value food item and the recipient could receive one high-value food item (vice versa in the advantageous condition); (2) reward inequity, in which the actor could receive one nonfood item and the recipient could receive one high-value food item (vice versa in the advantageous condition).

Apparatus

We constructed an apparatus that allowed subjects to accept or reject different resource allocations. The apparatus was made out of

Table 1
Food rewards for actor and recipient across different treatments in disadvantageous and advantageous conditions

	Disadvantageous		Advantageous	
Treatment	Actor	Recipient	Actor	Recipient
High equity	Kix	Kix	Kix	Kix
Low equity	Rice Krispie	Rice Krispie	Rice Krispie	Rice Krispie
Nothing equity	Peanut shell	Peanut shell	Peanut shell	Peanut shell
Quality inequity	Rice Krispie	Kix	Kix	Rice Krispie
Reward inequity	Peanut shell	Kix	Kix	Peanut shell

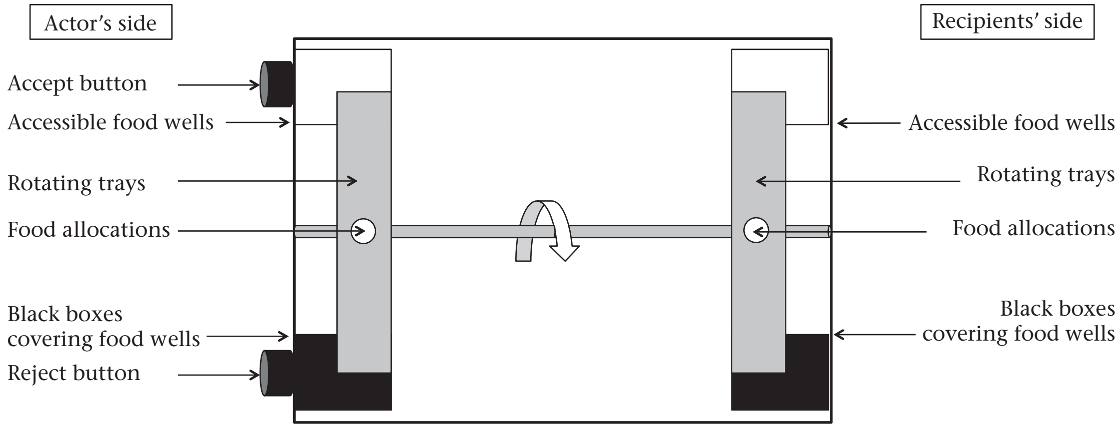

Figure 1. Bird's-eye view of the apparatus. Actors had access to two buttons that controlled a tray that rotated around a metal dowel (so that rewards could be tipped to the left or right). Reward allocations were placed on the trays and would fall into one of two food wells. If the actor accepted an allocation, both the actor and recipient could access the fallen food (accessible food wells). If the actor rejected an allocation, food items fell into compartments that were inaccessible to both the actor and recipient (food wells covered by black boxes).

two large squares of Plexiglas connected by four long metal rods (Fig. 1). Two large buttons (3.81 cm in diameter) were located on the actor's side the apparatus. There were no buttons on the recipient's side of the apparatus. Two small trays rested flush against the inside of the Plexiglas squares and were supported by a fifth metal rod that ran through the centre of both Plexiglas squares. Food items were placed in the centre of these trays. The rod was attached under the trays so that the trays could tilt simultaneously to the right or to the left. The two buttons controlled tray movement. If the actor pressed the right-side button, both trays would tip towards the right. If the actor pressed the left-side button, both trays would tip towards the left. Two food wells were located on each square of Plexiglas (thus, four wells in total, two on the right side of the apparatus and two on the left). These wells were located below the trays such that when the trays tipped towards the right or the left, they would deliver food items into either the two right or two left wells, respectively.

The apparatus was placed between two smaller testing chambers (0.8 m^3) so that the actor monkey could access the buttons and food wells through one chamber, and the recipient could access the food wells through the other chamber. The actor and recipient could always see each other and both individuals could see the food on the other side of the apparatus.

On every trial, monkeys could access the food wells on one side, but the food wells on the other side were covered by black boxes, making them inaccessible. Black boxes were made out of foamcore and black duct tape. The placement of the black boxes on either the two right-side wells or to the two left-side wells was counterbalanced within session. The accessibility of the food wells (i.e. the placement of the black boxes) determined whether the left or right button constituted the ‘accept’ or ‘reject’ button. Specifically, actors were free to push either the button on the left or the right. Depending on the location of the black boxes, an actor's button selection resulted either in ‘acceptance’ or ‘rejection’ of food items. For example, if the black boxes were covering the left-side wells, the actor could accept an allocation by pressing the right-side button, causing the trays to tip to the right and deliver food items to the right-side wells. Both the actor and recipient could then obtain food items from the right-side wells. If, on the other hand, the actor pressed the left-side button, the trays would tip to the left, delivering food to the covered wells, which neither monkey could access. This left-side button press would qualify as a rejection of the reward allocation. Critically, accepting and rejecting required the same action from the monkey, which ruled out the possibility that behavioural differences would be due to one action being more interesting than the other.

Procedure

Prior to experimental testing, actors were given (1) preference tests to ensure that they preferred the food we chose as highly valued (Kix cereal) over the food we chose as low valued (Rice Krispies cereal); (2) training to ensure that they understood how the apparatus worked; and (3) training to ensure that they understood the contingent payoff structure of the task.

Pre-test Sessions

Preference testing

We used two types of cereal as food rewards in this study. Kix™ were considered to be the high-value food reward and Rice Krispies™ the low-value food reward. To establish that all deciders perceived these rewards to be high and low value, respectively, we conducted food preference tests. Subjects were tested in a small testing chamber with two trading holes on opposite sides. Subjects had previously been trained to trade tokens with experimenters in exchange for food items. Subjects first received two forced-choice trials, in which they traded for one food type and then the other. We then administered 10 preference trials in which subjects chose between trading with two experimenters, each offering one of the food types. The location of the experimenter offering the high-value food item alternated across trials. Subjects had to demonstrate a robust preference for Kix over Rice Krispies, choosing Kix at least 8 out of 10 trials for two consecutive sessions, before being advanced to the training phase of the study.

Training phase 1

In training phase 1, we wanted to establish that each decider understood how the apparatus worked. Thus, in this phase we familiarized deciders with the apparatus and the black boxes (which prevented the monkeys from accessing food dropped in the wells). The black boxes always moved in parallel, and were both placed either on the right-side wells or on the left-side wells.

At the beginning of each training session, the subject was isolated in the smaller testing chamber on the left, with the apparatus placed next to it. At the start of each trial, a piece of cereal (Kix or Krispie) was placed on the tray closest to the subject monkey. Each session had 16 trials: eight trials with each reward type.

Additionally, on half the trials, the left-side wells were blocked, on the other half, the right-side wells were blocked. Reward type and blocked side were randomized within session. Subjects were required to push one of the buttons within 30 s. If the subject did not make a choice within 30 s, the experimenter removed the food and pushed the button for the open side in order to indicate the start of a new trial. The subject monkey was moved out of the smaller testing chamber between trials so that he/she would not interfere with resetting the apparatus. To pass this phase of training, monkeys had to choose the button that dropped the cereal into the open well for 13 out of 16 trials for two consecutive sessions. Subjects completed this phase within 9 and 13 sessions.

Training phase 2

In this phase, we wanted to ensure that deciders understood that their choices affected not only their own payoffs but also the recipients' payoff. The set-up was identical to the set-up in training phase 1 except that, here, a second smaller testing chamber was placed on the right of the apparatus such that the apparatus was between these two testing chambers (see Fig. 1). This smaller chamber would be the recipient's chamber during testing, but recipients were absent during training. On each trial, a food item was placed on the recipient's tray. After choosing to accept the food item, deciders had to go to the receiver side in order to access the food.

In the first part of this training phase, each session had 16 trials in which the black box alternated sides every four trials. In the second part of this phase, each session had 16 trials that were randomized and counterbalanced with regards to box side. To pass both parts of this training phase, deciders had to choose the button that delivered food to the recipient's open well on 13 out of 16 trials for two consecutive sessions. Subjects completed the first part of this phase within two to five sessions and second part of this phase within two sessions.

Test Sessions

At the start of each experimental session, the actor was located adjacent to the left-side testing chamber while the recipient was located adjacent to the right-side testing chamber. Once the monkeys were in position, the experimenter would attach the two black boxes to two of the food wells. Next, the experimenter would place reward allocations on the rotating trays. During social sessions, the experimenter would allow the actor and recipient to enter the left-side and right-side chambers, respectively. The actor then had access to both buttons. Once the actor had pressed a button, causing food to be dropped into either the uncovered well (an acceptance) or covered well (a rejection), he/she was given time to access and consume any food items in the uncovered well. Following food consumption, the actor was moved out of the testing chamber. The recipients, on the other hand, had continuous access to their chamber for the duration of the session. We allowed the recipients to have continuous access to their chamber, as opposed to moving the recipient in and out as we did with the actor, because we thought this would increase the salience of the social conditions. During nonsocial sessions, the metallic sliding door separating the recipient from the testing chamber was never removed, although the monkeys remained in visual contact. Consequently, the recipient could not access his/her testing chamber and thus could not access food items that were delivered to his/her well. Monkeys typically made their choice within 10 s (mean ± SD = 8.3 ± 10.5 s). To reduce frustration, if actors failed to make a timely choice within approximately 1 min, they were moved out of the testing chamber, the slider was replaced and their decision was recorded as ‘no choice’ (mean ± SD time of calling ‘no choice’ was 46 ± 15.5 s, calculated following the deletion of a single outlier due to coding error).

Coding and Analyses

Choice data were coded live by an experimenter and double-checked from video recordings (available for 96% of trials). Choices were coded as ‘accept’, ‘reject’ and ‘no choice’. Agreement between data from live and video coding was good (95% agreement, Kappa = 0.8). Any inconsistencies between live and video coding data were corrected by rechecking the video. Reaction time data were coded from video recordings. Reaction time was coded from the moment the actor had the opportunity to enter the testing chamber, which was marked by the removal of a metal slider, until they first touched the button that resulted in their choice. All available videos were coded for reaction times. An independent coder then coded a subset (20%) of videos. Agreement between coders was high (Pearson correlation: $r_{655} = 0.86$, $P < 0.001$; see Supplementary Material for details regarding reliability coding). In analyses, reaction times were only included for accept and reject decisions and were excluded for ‘no choice’ decisions.

Statistical analyses were conducted using R statistical software (version 2.15.2, R Foundation for Statistical Computing, Vienna, Austria). Subjects' choices were collapsed into a binary variable: accept or did not accept (did not accept was a composite of rejects (1% of trials) and no choice trials (11% of trials)) and analysed using generalized linear mixed models (GLMMs) with a binary response term (accepted = 1, did not accept = 0; Bolker et al., 2009). Analyses were also performed on decision data excluding cases in which subjects made no choice (see Supplementary Material). Reaction time data were log transformed and analysed using linear mixed models (LMMs), as the transformed response term had a normal error distribution. Predictors of interest were condition (disadvantageous, advantageous), treatment (high equity, low equity, nothing equity, inequity, reward inequity) and social context (social, nonsocial). To control for repeated measures, subject identity and session number were included in mixed models as nested random factors (session number was nested in subject identity; see Supplementary Fig. S2 for dependent measures plotted by session). All mixed models were run using R package ‘lme4’ (Bates, Maechler, & Bolker, 2012).

In mixed model analyses, we first examined a null model, which included only subject identity. We then compared the null models with full models that included predictor variables of interest. Model comparisons were conducted with likelihood ratio tests (LRTs).

Ethical Note

This project was approved by the Institutional Animal Care and Use Committee at Yale University (protocol number 2008-10678).

RESULTS

Our first question was whether subjects behaved differently depending on whether they were in the disadvantageous or advantageous condition. Examining the acceptance decisions, a GLMM of acceptance behaviour as a function of condition was a better fit to the data than a model that did not contain the condition term (LRT: $\chi^2_1 = 47.06$, $P < 0.001$). Similarly, condition was a significant predictor of subjects' reaction times (LRT: $\chi^2_1 = 5.11$, $P = 0.02$). Thus, subjects behaved differently in the two conditions. Given this, we performed subsequent analyses separately by condition.

Disadvantageous Inequity

Fig. 2a shows subjects' acceptance behaviour as a function of treatment in the disadvantageous condition. Decisions to reject or to not choose in the disadvantageous condition were relatively rare overall (16%) compared to decisions to accept (84% of trials). Subjects were most likely to accept allocations in the high equity condition (97%), less likely to accept in the low equity (88%) and inequity (87%) treatments and least likely to accept in the nothing equity (69%) and reward inequity (78%) treatments. Our model revealed that treatment was a significant predictor of subjects' acceptance behaviour (LRT: $\chi^2_4 = 141.47$, $P < 0.001$; see Supplementary Table S2 for model output). However, neither social context nor the interaction between social context and treatment was a significant predictor of subjects' decisions (LRT: $Ps > 0.6$). These results suggest that subjects' behaviour was driven not by relative food distribution or partner presence but rather by the type of food that they themselves would receive.

Fig. 3a shows subjects' reaction times across treatments in the disadvantageous condition. Subjects were relatively quick to make decisions (mean ± SD = 8.83 ± 10.94). Subjects' reaction times were affected by treatment (LRT: $\chi^2_4 = 277.55$, $P < 0.001$) but not by social context or the interaction between treatment and social context (LRT: $Ps = 1$). As Fig. 3a illustrates, subjects' reaction times aligned with the offered reward allocation: they were fastest in high equity, slower in low equity and inequity and slowest in nothing equity and reward inequity (see Supplementary Table S2 for model output).

Advantageous Inequity

Fig. 2b shows subjects' acceptance behaviour as a function of treatment in the advantageous condition. Again, decisions to reject or to not choose were relatively rare overall (8%) compared to decisions to accept (92%). Subjects showed high acceptance rates across high equity (98%), low equity (96%), inequity (98%) and reward inequity (97%) conditions. By contrast, subjects were relatively less likely to accept in the nothing equity condition (69%). Our GLMM showed that there was an interaction between treatment and social context (LRT: $\chi^2_4 = 12.48$, $P = 0.014$). However, this was a weak effect as is evidenced both by effect sizes (Supplementary Table S2) and by an examination of the data (Supplementary Fig. S3). The more striking result was that subjects were less likely to accept allocations in the nothing equity treatment (where both actor and recipient received nonfood items) compared the other treatments (Fig. 2b). Because of the weak interaction between social context and treatment, we were unable to isolate the effect of removing the treatment term. However, Supplementary Table S2 shows estimates for the treatment effects. Clearly, the largest effects were seen in comparisons between subjects' acceptances in the nothing equity condition and the conditions in which subjects received the high-value food reward.

Fig. 3b shows subjects' reaction times across treatments in the advantageous condition. Again, subjects were relatively quick to make decisions (mean ± SD = 7.88 ± 10.1 s). Treatment was a significant predictor of reaction time (LRT: $\chi^2_4 = 231.6$, $P < 0.001$). Neither social context nor the interaction between social context and treatment were significant predictors (LRT: $Ps = 1$). As in the disadvantageous condition, subjects' reaction times in the advantageous condition aligned with the reward allocations that were presented: subjects were fastest to make decisions when they were offered Kix (high equity, inequity, reward inequity), slightly slower when offered Krispies (low equity) and slowest when offered nonfood items (nothing equity).

Examining the Effects of Actor and Recipient Food Types

Our previous analyses suggested that actors' behaviour was not influenced by inequity aversion but rather was best predicted by the food that they received. To test this idea we conducted additional analyses that included actor and recipient reward types as separate predictor variables. Specifically, these models were conducted to test (1) whether actor food was indeed the best predictor of actor behaviour and (2) for potential effects of recipient food

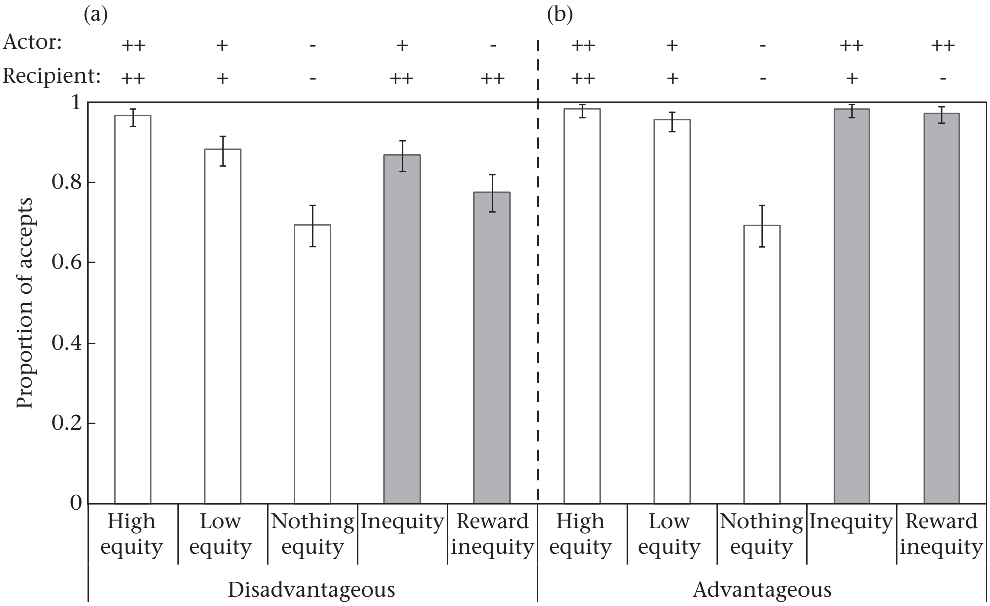

Figure 2. Subjects' acceptance behaviour across five treatments in (a) disadvantageous and (b) advantageous conditions. Equity treatments (white bars) were identical across disadvantageous and advantageous conditions. The direction of inequity treatments (grey bars) switched based on condition (disadvantageous: actor received relatively poor payoff; advantageous: actor received relatively good payoff). Actor and recipient rewards are indicated using the following notation: Kix (++); Rice Krispies (+); peanut shells (−). Error bars show binomial confidence intervals.

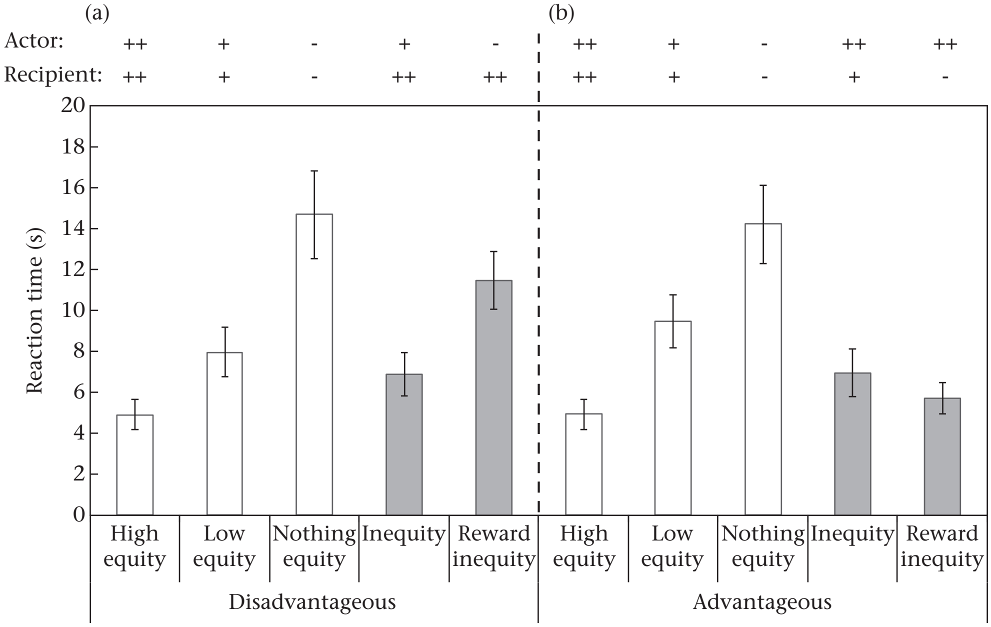

Figure 3. Subjects' reaction times (seconds) across five treatments in (a) disadvantageous and (b) advantageous conditions. Equity treatments (white bars) were identical across disadvantageous and advantageous conditions. The direction of inequity treatments (grey bars) switched based on condition (disadvantageous: actor received relatively poor payoff; advantageous: actor received relatively good payoff). Actor and recipient rewards are indicated using the following notation: Kix (++); Rice Krispies (+); peanut shells (−). Error bars show confidence intervals.

type. To this end, we recoded the treatment variable into two reward variables based on what the individual in each role received in a given treatment: (1) actor food reward (high quality: Kix; low quality: Krispie; nonfood: peanut shells); (2) recipient food reward (high quality: Kix; low quality: Krispie; nonfood: peanut shells).

Actor reward was a significant predictor of choice behaviour and reaction time in both disadvantageous (choice data, GLMM: $\chi^2_2 = 72.45$, $P < 0.001$; reaction time, LMM: $\chi^2_2 = 165.79$, $P < 0.001$) and advantageous conditions (choice data, GLMM: $\chi^2_2 = 118.97$, $P < 0.001$; reaction time, LMM: $\chi^2_2 = 173.85$, $P < 0.001$; see Supplementary Table S4 for model output). These results suggest that actor food reward did indeed predict actor behaviour (both choice and reaction time) in both conditions.

In addition, the food placed on the recipient's side was a significant predictor of choice behaviour in the disadvantageous condition (GLMM: $\chi^2_2 = 8.16$, $P = 0.02$) and of reaction time in both conditions (LMM: disadvantageous: $\chi^2_2 = 11.05$, $P = 0.004$; advantageous: $\chi^2_2 = 12.59$, $P = 0.002$). Thus, our analyses also suggest that the food placed on the recipient's side of the apparatus exerted an influence in some contexts.

To examine the potential effects of recipient reward type in more detail, we subsetted the data into cases in which the actor's payoff was the same but the food placed on the recipient's side varied. In the disadvantageous condition, this subset consisted of low equity and inequity trials (actor received Krispie, and the food placed on recipient side was Krispie and Kix, respectively) and a subset consisting of nothing equity and reward inequity trials (actor received peanut shell, and the food placed on recipient side was peanut shell and Kix, respectively). In the advantageous condition, this subset consisted of high equity, inequity and reward inequity trials (actor received Kix, and the food placed on recipient side was Kix, Krispie and peanut shell, respectively). These analyses revealed that the food placed on the recipient's side did exert an influence on actor's choice behaviour and reaction time. Specifically, in the disadvantageous condition, actors were less likely to accept allocations when the recipient received nonfood than when the recipient received Kix in the two treatments wherein the actor received peanut shells (nothing equity and reward inequity; see Supplementary Table S4 for effects; GLMM: effect of recipient food: $\chi^2_1 = 7.75$, $P = 0.005$). A subsequent model testing whether social context influenced this relationship revealed that social context was not a significant predictor of actor behaviour (GLMM: $\chi^2_1 = 0.35$, $P = 0.553$). In these same conditions, actors were slower to accept when their partner received a nonfood item compared to when their partner received Kix (see Supplementary Table S4 for effects; LMM: effect of recipient food: $\chi^2_1 = 7.02$, $P = 0.008$). Again, social context was not a significant predictor of actor behaviour (LMM: $\chi^2_1 = 0.83$, $P = 0.363$). In the advantageous condition, actors were slower to make a choice when their partner received a Krisipe or nonfood item compared to Kix in conditions in which the actor received Kix (high equity, inequity and reward inequity; see Supplementary Table S4 for effects; LMM: $\chi^2_1 = 15.54$, $P < 0.001$). Once again, social context was not a significant predictor (LMM: $\chi^2_1 = 0.90$, $P = 0.636$). In summary, monkeys were, in some treatments, influenced by the food placed on the other side of the apparatus. However, it did not matter whether or not this food was being delivered to a partner.

In summary, these analyses suggest that actor food type was a significant predictor of actor behaviour but that actors may have been, to some degree, additionally influenced by the food on the recipient's side of the apparatus.

DISCUSSION

Capuchins did not show disadvantageous or advantageous inequity aversion in our costly choice task. Subjects accepted the majority of presented allocations, regardless of distribution or partner presence. Subjects showed some variation in their propensity to accept allocations across conditions, but this variation was explained by food type: they were most likely to accept when they received a high-value food item, less likely to accept when they received a low-value food item, and least likely to accept when they received a nonfood item. Similarly, subjects' reaction times aligned with their food preference: they made decisions most quickly when offered high-value food and most slowly when offered a nonfood item.

Our finding that subjects did not show disadvantageous inequity aversion is difficult to reconcile with results from other capuchin monkey studies that have provided evidence for this form of inequity aversion (e.g. Brosnan & de Waal, 2003; van Wolkenten et al., 2007). One reason for this discrepancy may stem from the differences between our inequity task and the tasks used in prior studies. In previous studies, subjects engaged in a noncontingent trading task, in which actors' decisions affected their own, but not their partner's, payoff (Brosnan & de Waal, 2003; van Wolkenten et al., 2007). This meant that subjects could refuse their own unattractive offer but could not prevent partners from getting their more desirable allocation. Critically, refusals in this context increase the inequality between the two individuals (Henrich, 2004). By contrast, in our task, rejections eliminate the inequity between actor and recipient. It is possible that capuchin monkeys are only willing to sacrifice their own reward when doing so has no effect on their partner. This interpretation would align with results showing that capuchin monkeys deliver food to their partners in prosocial tasks (Lakshminarayanan & Santos, 2008) and sometimes prioritize preferences for increasing their partner's rewards over inequity concerns (Brosnan et al., 2010). If capuchin monkeys have strong prosocial preferences they may not have been motivated to take food away from their partners. In line with this view, capuchins in our study were more likely to accept allocations or abstain from making a choice rather than actively reject allocations. Nevertheless, this interpretation raises the question of why researchers tend to observe high rates of rejections in human inequity aversion tasks, particularly since humans are known for their strong prosocial preferences. One possible explanation for this tension is that humans may show competing motivations between prosociality and spite (a motivation we discuss below) in a way that nonhuman primates do not.

Regardless of the reason behind the low frequency of rejections in our task, our results hint at the possibility that apparent inequity aversion in capuchins is fundamentally different from inequity aversion in humans. Specifically, if capuchins reject inequity only in noncontingent tasks, the ‘goal’ of their rejections is both unclear and unlike the goal of inequity rejections in humans. In human adults and children, individuals are more likely to reject inequity when rejections affect their partner (i.e. in contingent tasks; Dawes et al., 2007; Güth et al., 1982; McAuliffe et al., 2015) than when their rejections have no affect on their partner (i.e. in noncontingent tasks; Hachiga, Silberberg, Parker, & Sakagami, 2008; but see Ostojić & Clayton, 2013). This suggests humans' rejections are motivated by spite, the willingness to pay to inflict a cost on another (Hamilton, 1970), rather than frustration at not being able to access the more attractive resource (McAuliffe et al., 2015). Our contingent task strongly suggests that capuchins do not reject inequity out of spite, leaving open the question of why they do occasionally reject allocations in noncontingent tasks. One possibility is that rejections in noncontingent tasks represent a signal to potential partners that disadvantaged individuals will not tolerate unfairness (Brosnan, 2011). Another possibility is that capuchins reject inequity in noncontingent tasks out of frustration (Roma et al., 2006; Silberberg, Roma, Ruggiero, & Suomi, 2006; Silberberg et al., 2009). Indeed, socially enhanced frustration (i.e. frustration that is made more salient by the presence of a social partner receiving the better food) could explain the higher frequency of inequity refusals in social tests versus nonsocial controls in previous work on inequity aversion in capuchin monkeys (e.g. Brosnan & de Waal, 2003). It is interesting that we did not see evidence for socially enhanced frustration in our task, but we suspect that this may be because actors were not made to watch their partner eat the higher-quality food prior to making their decision as in previous studies. Whatever the reason for rejections in nonsocial tasks, be it socially enhanced frustration or signalling to partners, future work could begin to address capuchins' motivations by directly comparing tasks with contingent and noncontingent payoff structures.

Not only did capuchins in our study fail to reject disadvantageous inequity but they also failed to reject advantageous inequity, cases where they received more than their partner. This pattern of performance is perhaps not surprising for two reasons. First, the positive fitness consequences of giving up relatively good resource allocations are difficult to imagine, which, a priori, makes it unlikely that animals would exhibit advantageous inequity aversion. Second, while disadvantageous inequity aversion emerges early in human development, advantageous inequity aversion emerges relatively late (Blake & McAuliffe, 2011; Shaw & Olson, 2012), indicating that the two forms of inequity aversion are decoupled in ontogeny and may thus be decoupled in phylogeny as well. Nevertheless, prior work has not tested systematically advantageous inequity aversion outside of humans. Previous studies have tested indirectly advantageous inequity aversion in nonhuman animals: in the noncontingent trading task described above, recipients could, in principle, refuse their desirable allocation. In line with this, there is some evidence that chimpanzees do occasionally refuse advantageous allocations (Brosnan et al., 2010). However, these results are difficult to align with advantageous inequity aversion tests in humans because, again, the tasks are not contingent. Thus, the present study is the first to directly test advantageous inequity aversion in a nonhuman animal species in a task that is comparable to human tasks.

Our findings indicate that capuchin monkeys are unwilling to sacrifice personal gain to prevent a partner from receiving a more desirable (disadvantageous) or less desirable (advantageous) reward allocation. These results contrast with those found in human adults and children. Adult results show that individuals readily sacrifice personal rewards to prevent both forms of inequity (Dawes et al., 2007). Developmental research in humans shows that from a young age, children are willing to sacrifice personal gain to prevent disadvantageous allocations and later show an aversion to advantageous allocations (Blake & McAuliffe, 2011; McAuliffe et al., 2013; Shaw & Olson, 2012). A key feature of results from adult and child inequity aversion studies is that subjects' decisions about whether or not to accept a reward allocation are influenced both by their partner's allocation (i.e. the relative resource distribution) as well as by the social context (McAuliffe et al., 2013; Sanfey, Rilling, Aronson, Nystrom, & Cohen, 2003). In contrast, while our subjects were influenced by the food placed on the recipient's side of the apparatus, they seemed to be making decisions that were unaffected by their partner's presence. Overwhelmingly, our results indicate that capuchins' behaviours were guided primarily by the food type that they were offered, indicating that their decisions and reaction times were reflective of their food preferences and motivation as opposed to their responses to inequity.

One possible explanation for these findings is that subjects were simply attending to the food on their side of the apparatus and were ignoring the food items on their partner's side. However, we do not favour this explanation for the following reasons. First, subjects had to demonstrate their understanding of our task's contingent payoff structure during training (see Supplementary Material for training procedures). During the second phase of training, subjects were offered an allocation in which they received no food while a high-valued food item was placed on the opposite tray. To pass this phase, subjects had to accept the allocation and retrieve the food item from the recipient's enclosure. Given that all of our subjects passed this training, we are confident that they both attended to the food on the recipient's side of the apparatus and understood the contingency between their button choice and food delivery to the recipient's side. However, a possible limitation of this training phase is that subjects could pass this phase by learning to attend to food that was placed on the recipient's side only when there was no food on their own side. Fortunately, our results revealed that subjects were attending to their own allocation and the recipient's allocation simultaneously. Specifically, we found that the food placed on the recipient's side of the apparatus did, in some treatments, influence actor choices and reaction times. If actors were attending solely to the food on their own side, then we would not expect the recipient food type to exert any influence on their behaviour. Given these two findings, we suspect that subjects' infrequent rejections were probably not due to a lack of understanding of the task but rather were due to an indifference towards the relative payoff between themselves and a partner. While these lines of evidence indicate that subjects were attending to the food on both sides of the apparatus, it is possible that subjects may not have perceived our task as truly social. In the absence of significant differences between the social and nonsocial contexts, it is impossible to demonstrate conclusively that they viewed our task as a social problem. Moreover, given that actors' decisions were overwhelmingly determined by the food placed on their side of the apparatus, it is difficult to say for certain that their frequent acceptance behaviour was due to a lack of concern for, as opposed to a lack of knowledge of, food on the recipient's side. With that caveat in place, our results suggest that even when the costs of rejection were very low (i.e. in the reward inequity treatment in the disadvantageous condition), subjects were not motivated to deprive their partner of a more desirable payoff.

Another possible limitation of our study concerns the subject population of capuchins available for testing. First, we were only able to test one male actor. It is possible that this bias towards female subjects may have skewed our results, as sex effects on inequity aversion have been reported (Hopper et al., 2014). An additional limitation concerns our use of subordinate individuals to the recipient role. While dominance effects on inequity aversion are rare (but see Massen et al., 2012; Melis, Hare, & Tomasello, 2009), manipulating the dominance relationship between actor and recipient would be an interesting area for future work.

A final possible limitation of our task is that we required minimal effort on the part of the actors: pressing a button is relatively easy, although in our view such button presses are comparable in effort to token trading. Effort has been suggested to be an important mediator of inequity aversion in animals (van Wolkenten et al., 2007), although when carefully manipulated, the effects of effort are not straightforward (Massen et al., 2012; McAuliffe, Shelton, & Stone, 2014). Nevertheless, it is possible that our task may have been more aversive to subjects if the actors had to pay a large cost to deliver a better payoff to a partner.

In summary, we found no evidence for disadvantageous or advantageous inequity aversion in capuchin monkeys tested on a contingent costly choice task. This task closely mirrored work conducted with humans and thus provides an opportunity to directly compare human and nonhuman animal inequity aversion results. Our results suggest that apparent inequity aversion in capuchins is fundamentally different from that expressed by human adults and children. More broadly, our results hint at the possibility that the links that have been drawn between inequity aversion in humans and nonhuman animals may be weaker than we think.

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Supplementary Material

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