



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



Katherine McAuliffe^{a, *}, Linda W. Chang^a, Kristin L. Leimgruber^a, Rebecca Spaulding^a, Peter R. Blake^b, Laurie R. Santos^a

^a Department of Psychology, Yale University, New Haven, CT, U.S.A.

^b Department of Psychology, Boston University, Boston, MA, U.S.A.

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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.

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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

* Correspondence: K. McAuliffe, Department of Psychology, Yale University, New Haven, CT 06520-8205, U.S.A.

E-mail address: katherine.mcauliffe@yale.edu (K. McAuliffe).

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, Crescimbeni, Addressi, 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

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