Evolution and Human Behavior xxx (2013) xxx–xxx

Contents lists available at ScienceDirect

Evolution and Human Behavior

journal homepage: www.ehbonline.org

Original Article

# Capuchin monkeys (*Cebus apella*) fail to show inequality aversion in a no-cost situation

Mark Sheskin *, Kim Ashayeri, Amy Skerry, Laurie R. Santos

*Department of Psychology, Yale University, New Haven, CT, USA*

ARTICLE INFO

*Article history:*
Initial receipt 23 December 2012
Final revision received 25 October 2013
Available online xxxx

*Keywords:*
Capuchin monkeys
Inequality aversion
No-cost situation

ABSTRACT

Although humans show robust equality concerns across a variety of situations, there is ongoing debate regarding the extent to which any nonhuman species is inequality averse. In the current research, we test nonhuman primates' reactions to conspecifics receiving equal and unequal payoffs using a "no-cost" method in which subjects can respond to inequality without rejecting food. Specifically, we gave capuchin monkeys (*Cebus apella*) the opportunity to trade with one of two experimenters, each of whom offered the subject an identical reward, but had different histories of trading with the subject and a conspecific partner. An "equal" experimenter had previously given a conspecific the same reward that the subject had received, whereas the other experimenter was either an "advantageous trader" for the subject (giving the conspecific an inferior reward) or a "disadvantageous trader" for the subject (giving the conspecific a superior reward). By offering subjects a choice between experimenters, we removed several competing demands that may have masked the expression of robust equality preferences in previous studies. Even though there was no cost associated with expressing an equality preference, we found no evidence that capuchins differentiated between equal and unequal experimenters.



## 1. Introduction

Fairness is a central concern for the human species (Haidt & Joseph, 2004; Henrich et al., 2005; Henrich et al., 2006; Haidt & Joseph, 2007; Henrich et al., 2010). In many cases, humans are willing to take costs to ensure that situations are equitable (Guth, Schmittberger, & Schwarze, 1982; Kahneman, Knetsch, & Thaler, 1986; Fehr & Schmidt, 1999; Camerer & Foundation, 2003), particularly when they would otherwise be at a relative disadvantage (e.g., Zizzo & Oswald, 2001). Disadvantageous inequality aversion—reacting negatively to receiving less than someone else—is present even in young children (Gerson & Damon, 1978; Birch & Billman, 1986; Sigelman & Waitzman, 1991; Fehr, Bernhard, & Rockenbach, 2008; Olson & Spelke, 2008; LoBue, Nishida, Chiong, DeLoache, & Haidt, 2009). Older children (Blake & McAuliffe, 2011; Shaw & Olson, 2012) and adults (Tricomi, Rangel, Camerer, & O'Doherty, 2010; Zaki & Mitchell, 2011) also show "advantageous inequality aversion" against situations in which others receive less than themselves.

It remains controversial whether nonhuman primates (hereafter, primates) also react negatively to unequal situations. Studies using a variety of experimental designs have yielded conflicting evidence concerning whether primates attend to others' payoffs, and (if they do) whether they have preferences regarding the equality of payoffs. Some studies have reported that primates are sensitive to inequality when choosing food distributions for self and a conspecific, preferentially choosing equitable distributions (capuchins *Cebus apella*: Fletcher, 2008; de Waal, Leimgruber, & Greenberg, 2008; chimpanzees: Horner, Carter, Suchak, & de Waal, 2011; Proctor, Williamson, de Waal, & Brosnan, 2013; marmosets *Callithrix jacchus*: Burkart, Fehr, Efferson, & van Schaik, 2007), while others have found that primates choose relatively higher rewards for a conspecific rather than being averse to the inequality (capuchins: Lakshminarayanan & Santos, 2008), or are indifferent to another individual's payoff altogether (chimpanzees *Pan troglodytes*: Silk et al., 2005; Jensen, Call, & Tomasello, 2007; cotton-top tamarins *Saquinus oedipus*: Cronin, Schroeder, Rothwell, Silk, & Snowdon, 2009). This conflicting pattern of results has led to debate concerning the sensitivity of donation tasks to inequality aversion primates may possess (see debate in, for example, Jensen, Call, & Tomasello, 2013; Proctor et al., 2013b).

In a seminal study, Brosnan and de Waal (2003) developed a method (now widely used) to test primates' reactions to situations of inequality. Brosnan and de Waal presented capuchin monkeys with the chance to trade tokens for low-quality food rewards after first witnessing a conspecific partner performing a similar trade. When the partner received a relatively higher payoff, and especially if the partner was not required to first trade a token, subjects showed increased refusals to exchange tokens and increased rejections of their food payoffs relative to when the partner received the same low-quality reward as the subject (for a similar pattern of results with two populations of chimpanzees, see Brosnan et al., 2010a; Brosnan, Schiff, & de Waal, 2005).

* Corresponding author. Department of Psychology, Yale University, 2 Hillhouse Ave New Haven, CT 06520, USA.
*E-mail address:* mark.sheskin@yale.edu (M. Sheskin).

1090-5138/$ – see front matter © 2013 Elsevier Inc. All rights reserved.
http://dx.doi.org/10.1016/j.evolhumbehav.2013.10.004

Brosnan and colleagues have interpreted these results as evidence that capuchins are averse to disadvantageous inequality. However, such results are also consistent with the alternative explanation that primates react negatively to receiving a lesser reward than expected, independent of whether the expectation is set by seeing a conspecific receiving a high reward (see, for example, Tinklepaugh, 1928; see discussion in Chen & Santos, 2006). Thus, several studies have included control conditions to test whether negative reactions depend on whether the higher-value item goes to a social partner. For example, the original study by Brosnan and de Waal (2003) used a nonsocial control condition in which subjects saw higher-value rewards being delivered to an empty chamber. As clarified by a later analysis (Brosnan & de Waal, 2004), rejections increased over the course of the 25-trial social test condition in which the partner was present, but decreased over the course of the 25-trial nonsocial control condition in which the partner was absent. Brosnan and colleagues interpret this pattern as evidence that subjects became increasingly distressed at repeatedly being given a lower-value reward relative to a partner monkey during the test condition, but during the control condition either came to expect the lower-value reward or otherwise overcame the frustration of repeatedly receiving a less-than-expected reward. Studies using related methods have found evidence of disadvantageous inequality aversion in chimpanzees (Brosnan et al., 2005; Brosnan, Talbot, Ahlgren, Lambeth, & Schapiro, 2010), tamarins (Neiworth, Johnson, Whillock, Greenberg, & Brown, 2009), long-tailed macaques (Massen, Van Den Berg, Spruijt, & Sterck, 2012) and even non-primate species such as domestic dogs (*Canis familiaris*, Range, Horn, Viranyi, & Huber, 2009; Range, Leitner, & Virányi, 2012) and crows and ravens (Wascher & Bugnyar, 2013).

However, other studies using similar designs have either failed to find rejections in unfair situations, or have failed to replicate this difference between test and nonsocial control conditions, suggesting that nonhuman inequality concerns may be less robust than indicated by initial findings (e.g., Dubreuil, Gentile, & Visalberghi, 2006; Roma, Silberberg, Ruggiero, & Suomi, 2006; Silberberg, Crescimbene, Addessi, Anderson, & Visalberghi, 2009, but see Brosnan & de Waal, 2006; Dindo & de Waal, 2007; Hopper, Lambeth, Schapiro, Bernacky, & Brosnan, 2013; Massen et al., 2012). Dubreuil and colleagues (2006), for example, found that capuchins given a low-value reward rejected this reward at the same rate when a higher-value reward was given to a conspecific and when a higher-value reward was simply out of reach. Furthermore, Silberberg and colleagues (2009) found that capuchins accepted nearly every low-value trade, regardless of whether or not a higher-value reward was given to another monkey. Finally, Bräuer, Call, and Tomasello (2009) failed to find evidence of inequality aversion using nearly the same chimpanzee inequality aversion paradigm originally used by Brosnan and colleagues (2005).

### 1.1. Food-rejection methods and inhibitory control

In the current study, we explore the possibility that the null results reported by several previous studies (e.g., Bräuer et al., 2009; Silberberg et al., 2009) might be due to the high cost of the dependent measure typically used to assess equality preferences. Specifically, many previous studies have used a dependent measure based on food rejection (hereafter "food-rejection method"), in which subjects can exhibit inequality aversion by either refusing an opportunity to trade for food or by rejecting an otherwise tasty food reward. Tasks that require inhibiting prepotent desires can be challenging for primates (Addessi, Paglieri, & Focaroli, 2011; Anderson, Kuroshima, & Fujita, 2010; Boysen & Berntson, 1995; Diamond & Goldman-Rakic, 1989; Evans, Beran, Paglieri, & Addessi, 2012; Pelé, Micheletta, Uhlrich, Thierry, & Dufour, 2011, although see Amici, Aureli, & Call, 2008; Beran et al., (in press); Dufour, Pelé, Sterck, & Thierry, 2007; Rosati, Stevens, Hare, & Hauser, 2007; Stevens, Rosati, Heilbronner, & Mühlhoff, 2011 for cases where primates perform well). The demand of inhibiting desire for a food reward might prevent primates from expressing equality preferences in food-rejection methods. Consider, for example, some primates' performance on one common method for assessing inhibitory control— the "delay of gratification task." In this task, subjects must actively avoid an obtainable lesser reward while waiting for a larger reward to become available. Although some primates, like chimpanzees, succeed on such delay of gratification tasks (e.g., Beran et al., in press), other primates, like capuchin monkeys, perform quite poorly (e.g., Anderson et al., 2010; Pelé et al., 2011; Evans et al., 2012). Primates also tend to perform poorly on other tasks that make demands on inhibitory control, such as reverse-reward contingency tasks, in which subjects must pick the lesser of two rewards to obtain the one that is greater. Boysen and Berntson (1995), for example, found that chimpanzees could not learn to select the lesser of two rewards when the small reward was present, but were easily able to solve this task when less tempting abstract symbols were used in place of the rewards. For these reasons, it is possible that food-rejection methods may pose unnecessary tasks demands for some primate species (for similar inhibitory problems in a related task, see Jensen et al., 2007; Melis et al., 2011),

### 1.2. A no-cost preference measure

In the present study, we avoid pitting equality preferences against a prepotent desire, using a method that allows the subject to express an aversion to inequality without rejecting food or taking any other cost. In this "no-cost" method, primate subjects choose between two experimenters: one who has previously behaved fairly, giving equal rewards to the subject monkey and a partner monkey, and one who has previously behaved unfairly, giving unequal rewards. This method builds on previous studies demonstrating that some primates react differently to social agents based on observed third-party interactions (Herrmann, Keupp, Hare, Vaish, & Tomasello, 2012; Marshall-Pescini, Passalacqua, Ferrario, Valsecchi, & Prato-Previde, 2011; Russell, Call, & Dunbar, 2008; Subiaul, Vonk, Okamoto-Barth, & Barth, 2008; but see Brosnan & de Waal, 2009 for evidence of limits on these sorts of representations). For example, Russell and colleagues (2008) tested whether chimpanzees formed positive or negative impressions of human agents based on the agents' interactions with a third party. They found that a chimpanzee spent more time near a human who had previously been seen giving grapes to a beggar human, compared to a human who had not given grapes to this third party. Similarly, Subiaul and colleagues (2008) found that, with repeated exposure, chimpanzees came to preferentially beg from humans who had acted generously toward either a human or another chimpanzee. Herrmann and colleagues (2012) found a similar effect in chimpanzees and orangutans (*Pongo pygmaeus*); their subjects preferred to approach an experimenter who had previously been nice to a third party (tried to give food) over one who had been mean (prevented the food transfer via theft). Finally, Marshall-Pescini and colleagues (2011) found that dogs also preferentially approach humans who have been observed being generous with their food.

Taken together, these results suggest that some primates can keep track of other agents' behaviors based on how they treat other individuals. To date, however, only one study has extended this choice method to questions of inequality aversion. Horowitz (2012) tested whether dogs reliably distinguished between an experimenter who gave the subject and a partner conspecific equal rewards and an experimenter who gave a higher-valued reward to the partner than the subject. She found that dogs preferred a human who had over-rewarded the partner, suggesting that dogs make their choices on the basis of the potential for higher rewards rather than an aversion of inequality. Here, we extend this sort of method to the question of primate inequality aversion. Specifically, we tested whether capuchin monkeys would form preferences for one agent over another based on a history of equal or unequal trading.

Please cite this article as: Sheskin, M., et al., Capuchin monkeys (*Cebus apella*) fail to show inequality aversion in a no-cost situation, *Evolution and Human Behavior* (2013), http://dx.doi.org/10.1016/j.evolhumbehav.2013.10.004

### 1.3. Additional benefits of a preference measure

Note that the primary advantage of the preference measure we use in the current studies is that it allows subjects to potentially express inequality aversion in a situation that does not require inhibitory control. An experimenter-preference measure has three additional features that may provide greater sensitivity to equality concerns than rejection-based methods.

First, because expressing an experimenter preference does not require any cost, it can potentially pick up relatively weak preferences that food-rejection methods might miss. Even a subject with perfect inhibitory control might choose to accept a trade if the value of the food reward is greater than the aversion to the inequality. For example, consider the study by Silberberg et al. (2009), in which subjects accepted nearly every trade in both the test and nonsocial control conditions. In addition to showing no difference between the conditions, subjects also did not show the typical frustration effect after receiving less than an expected reward in a nonsocial situation (Tinklepaugh, 1928). This suggests the possibility that the value of the food rewards used by Silberberg et al. (2009) was high enough to counteract any frustration or equality motivations on the part of the subject. Humans show inequality aversion for goods that are both high value (e.g., water when thirsty, Wright et al., 2012) and low value (e.g., low values of money in a standard dictator game), but primates might have weaker equality concerns that are only detectable when there are not competing demands. Here, the food reward was regardless of the subject's choice, allowing even subtle preferences to be expressed. Indeed, as pointed out by Henrich (2004), food-rejection studies may not be an appropriate measure of inequality aversion, as rejecting a food reward *increases* inequality. However, there is a concomitant drawback of a preference measure: because the two experimenters provide identical rewards to the subjects over many days, initial preferences distinguishing the experimenters might decrease over time.

A second advantage of a preference method concerns its ability to detect both preferences and aversions based on equality concerns. Food-rejection methods used to date have only measured subjects' negative reactions— rejections of opportunities to trade— whereas a preference measure can detect positive reactions as well. It is plausible that capuchins may form a preference in favor of the disadvantageous trader—indeed, the dogs in Horowitz (2012) preferred the human who provided a better payoff to the partner.

A final strength of a preference measure is that it is well suited to test a previously understudied aspect of inequality aversion: whether primates avoid advantageous inequality as well as disadvantageous inequality. To date, few studies have explored whether primates avoid cases in which others receive *less* than they do. The tendency to avoid cases in which another individual is cheated relative to oneself is rather late-developing capacity in human ontogeny (Blake & McAuliffe, 2011; Shaw & Olson, 2012), and so may be present only weakly in primates (see Brosnan, 2006; Brosnan, 2008). If primates are only weakly averse to advantageous inequality, this preference is most likely to be detected using a no-cost preference method in which inhibitory control is not necessary and weak preferences do not compete with a cost. Furthermore, given that advantageous inequality is understudied, a no-cost preference measure allows for a research design that investigates equally the alternative that subjects will prefer that a conspecific receive a lesser reward than themselves and the alternative that subjects will prefer that a conspecific receive an equal reward as themselves.

### 1.4. The current study

In the present study, we employed this no-cost preference method to study capuchin monkeys, a primate species that has long been a focus of comparative work on inequality aversion (see review in Brosnan, 2006). Importantly for our method, previous work has shown that capuchins can reliably choose between two human traders based on preferences they have developed from watching the traders' previous behavior (e.g., Paukner, Suomi, Visalberghi, & Ferrari, 2009). However, to further verify that each subject could express preferences in our method, we first required that they pass a "basic choice" condition (see Fig. 1 for an overview of the entire method, and Section 2.4.1 for more detail about this condition).

To test both advantageous and disadvantageous inequality aversion, the main study presented our capuchin subjects with two types of conditions. The first type tested disadvantageous inequality (DI) aversion by giving subjects a choice of receiving a grape either from an equal trader, who also gives the partner a grape, or from a disadvantageous trader (DT), who gives the partner a higher-value marshmallow treat. The second type tested advantageous inequality (AI) aversion by giving the subjects a choice of receiving a grape either from an equal trader or from an advantageous trader (AT), who gives the partner a lower-value cucumber. As in several food-rejection studies (e.g., Brosnan & de Waal, 2003; Brosnan et al., 2005; Bräuer, Call, & Tomasello, 2006), we included a set of nonsocial control conditions to ensure that any responses we observed were not solely due to frustration at receiving a worse-than-expected reward, or to preferences based on the quality of rewards associated with different traders. These conditions were identical to the DI and AI conditions, except that an opaque bucket replaced the partner monkey (the rewards were placed into the bucket rather than being given to the partner monkey). This created a $2 \times 2$ design in which we varied both who received the alternative reward (*social* conditions in which another monkey received the reward versus *nonsocial* bucket controls) as well as the kind of reward given to the other individual (DI conditions in which a DT delivered a higher-value reward to the partner/bucket, or AI conditions in which an AT delivered a lower-value reward to the partner/bucket). Each subject completed all conditions in an order counterbalanced across subjects.

Several sets of results are plausible. Some have argued that human fairness concerns support the selection of social interaction partners who will provide high benefits, but also avoid being taken advantage of by providing disproportionate benefits to others (Baumard, André, & Sperber, 2013). If capuchins likewise have equality preferences, these preferences might be expected to reveal themselves in a preference for the equal trader over the disadvantageous trader who previously provided relatively higher rewards to the partner monkey, and we might additionally find a preference for the equal trader over the advantageous trader. On the other hand, capuchins might be more influenced by prosocial motivations (e.g., Lakshminarayanan & Santos, 2008) or image scoring (e.g., Russell et al., 2008), selecting an experimenter who has been observed to provide benefits for a third party. Indeed, using a similar method to our own, Horowitz (2012) found that dogs preferred the human who provided high rewards for the partner, even though these benefits were disadvantageously unequal for the subject.

## 2. Methods

### 2.1. Subjects

We tested four adult brown capuchin monkeys (AG, HG, HR, and JM). This number is similar to several previous studies of primate equality preferences: for example, Roma et al. (2006) tested four capuchins and Brosnan and de Waal (2003) tested five capuchins, though it is smaller than several other studies (e.g., Brosnan et al., 2005; Bräuer et al., 2009). Our subjects were a subset of the socially housed colony at the Yale Comparative Cognition Laboratory. One additional monkey, the alpha male (FL), served as the partner throughout the study (for considerations of how this impacted results, see Section 4). Other monkeys in our colony could not be

Please cite this article as: Sheskin, M., et al., Capuchin monkeys (*Cebus apella*) fail to show inequality aversion in a no-cost situation, *Evolution and Human Behavior* (2013), http://dx.doi.org/10.1016/j.evolhumbehav.2013.10.004

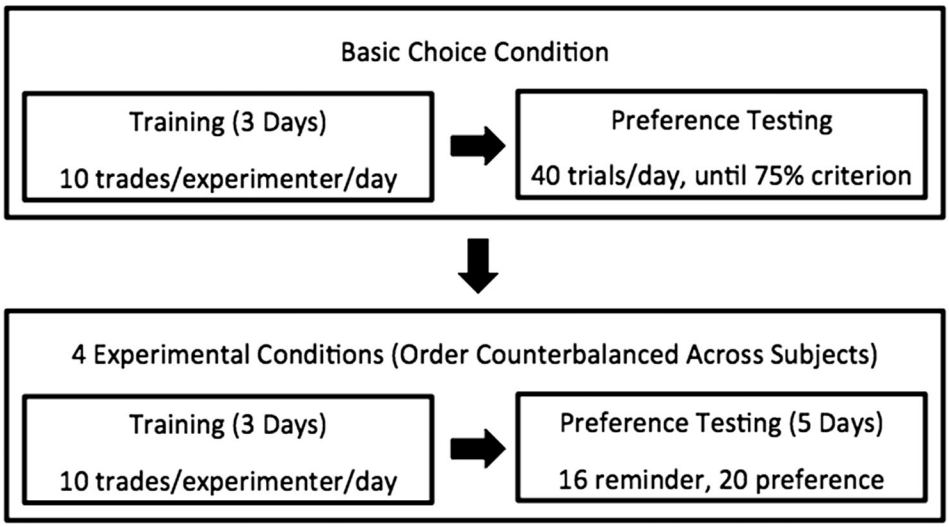


**Fig. 1.** Overview of the protocol. Each monkey first completed a "Basic Choice" condition consisting of 3 days of training and 3–4 days of preference testing (until showing a 75% preference for the higher-value trader across 2 days). Each monkey then completed each of the experimental conditions, in an order counterbalanced across monkeys. Each condition began with 3 days of training, and then included 5 days of preference testing. Each day of preference testing included 16 reminder trials and 20 preference trials.

tested either because they were unfamiliar with token trading or because they were uncomfortable trading in close proximity to the alpha male.

### 2.2. Set-up

#### 2.2.1. Enclosure

Subject monkeys were tested in two different locations (see Fig. 2). The training sessions for each condition took place in a familiar testing enclosure ($3 \times 3 \times 1$ m) that was adjacent to the main social cage. Throughout training (see Fig. 2, left), the partner monkey remained in the main cage, where he voluntarily sat adjacent to the testing enclosure during the session. As the partner was the alpha male, he was able to sit in the main cage and receive tokens and trade them for food without interference from other monkeys. Preference test sessions (see Fig. 2, right) took place away from the partner in a 0.8-$m^3$ side testing chamber attached to the testing enclosure. This side chamber was small enough that a monkey could reach experimenters standing on either side of the chamber (see Fig. 2, right). In this way, the position of the side chamber allowed subjects to choose between two experimenters simultaneously. In order to allow for visibility of the main cage, the side chamber was not closed off from the testing enclosure, and the subject was free to move between the side chamber and the testing enclosure.

#### 2.2.2. Food rewards

Experimenters traded tokens for one of three treats, each of which had a different value for the monkeys. The *high-value reward* was a

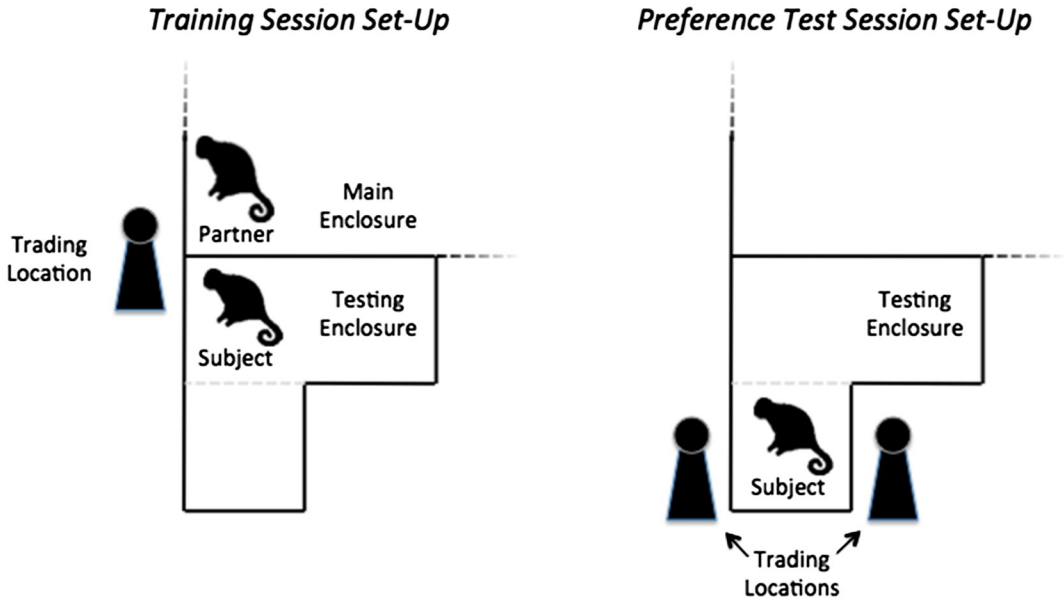


**Fig. 2.** A depiction of the enclosure and set-up used during the training and test sessions. During training sessions (left), the experimenters traded with both the subject and the partner (or bucket in the case of the nonsocial control condition) on the side of the enclosure. The experimenters took turns occupying the one trading location. During preference test sessions (right), the traders interacted only with the subject from the side chamber that was attached to the testing enclosure. The experimenters were present simultaneously, and alternated sides on each trial.

Please cite this article as: Sheskin, M., et al., Capuchin monkeys (*Cebus apella*) fail to show inequality aversion in a no-cost situation, *Evolution and Human Behavior* (2013), http://dx.doi.org/10.1016/j.evolhumbehav.2013.10.004

large marshmallow-filled "dumpling," consisting of a pouch of 1/12 of Fruit Roll-Up (a flat pectin-based fruit-based candy) filled with Marshmallow Fluff (a marshmallow crème spread). The *medium-value reward* was one half of one grape. The *low-value reward* was 1/8 of a cucumber slice. The medium- and low-value rewards were routinely part of the monkeys' diet, whereas Marshmallow Fluff and Fruit Roll-Up were provided very sparingly. However, each monkey had previously been exposed to these ingredients independently, as well as together. We further made sure that the subjects each had at least one high-value "dumpling" several days before the beginning of the study.

We conducted preference trials with each monkey to verify that their preferences reflected these reward levels. Each monkey was offered 10 choices between each pair of rewards (low- or medium-value, or medium- or high-value). All five monkeys preferred the medium-value to the low-value reward 100% of the time. This is a significant preference for each monkey (binomial test, $p < .001$). Four monkeys preferred the high-value over the medium-value reward 100% of the time (binomial test, $p < .001$). One of the monkeys (Holly) did not show this preference significantly, choosing the higher-value reward only 70% of the time (binomial test, $p = .172$).

Importantly, the preference trials to verify food preferences were conducted *after* the main study. Previous studies have suggested that frustration at not receiving a reward that had been previously provided in a study may account for some purported significant results (e.g., Silberberg et al., 2009). To avoid this concern, we never provided the subjects with the high-value reward used in our study (marshmallow "dumpling"), though each subject knew what it was from limited availability of the treat outside of the experimental setting.

#### 2.2.3. Presentation materials

Food was displayed to monkeys on 10-cm × 25-cm metal planks. Each experimenter always presented both possible treats on a plank (grape and cucumber when the unequal trader was an AT who gave cucumber to the partner, and grape and dumpling when the unequal trader was a DT who gave dumpling to the partner). The treats were always presented on the same sides of the plank for each experimenter.

### 2.3. Procedure

#### 2.3.1. General set-up

Three people ran each session: two experimenters acted as traders and one experimenter, who did not trade, gave the monkeys their tokens and recorded information about the session. In each condition, traders were novel individuals who were unfamiliar to the monkeys, ensuring that the monkeys had no existing preferences at the start of training. Thus, across the basic choice condition and the four experimental conditions, five pairs of new individuals interacted with a subject. When a pair of traders interacted with more than one subject, their behavior (equal or unequal) was counterbalanced across subjects. The two traders always wore different colored clothing in order to further distinguish themselves, and the colors each wore were the same across each day of a condition.

All conditions of the experiment involved two different periods: there were first three "training sessions," which were followed by five "preference-testing sessions." During the training sessions, subjects were introduced to two unfamiliar human traders who traded tokens for food rewards both with the subject and with the partner/bucket. The goal of the training sessions was for subjects to learn that both traders would give the subject identical rewards, and that the equal experimenter gave the partner/bucket the same treat whereas the unequal experimenter gave the partner/bucket a different treat. The five preference-testing sessions tested subject preferences between the traders by allowing the subject to choose which of the two experimenters to trade with. More detail is provided about these two different periods of each condition in Sections 2.3.2 and 2.3.3, followed by a description of the different types of conditions in Section 2.4.

#### 2.3.2. Training sessions

At the beginning of each training session, the subject was allowed to enter the testing enclosure. In test conditions, the partner was then encouraged by the non-trading experimenter to position himself adjacent in the main cage adjacent to the testing enclosure. The encouragement consisted in showing (but not providing) treats, and was typically not necessary after the partner learned to expect treats during this protocol at the correct location. In nonsocial control conditions, a bucket was affixed to the outside the cage at the location where the partner would usually trade. Thus, both monkeys could see each other through the cage in the social conditions, and the subject could see the bucket in the nonsocial conditions.

At the beginning of each trial in the social condition, the partner and the subject were each handed a token by the non-trading experimenter, who then stepped to the side. Once the monkeys each had a token, one of the two traders stepped closer to the enclosure, holding one hand outstretched while simultaneously displaying a set of food rewards with the other hand. The outstretched hand was within reach of only one of the monkeys, and was the signal that the trader was ready to trade (for more on the token trading method with this population, see Chen, Lakshminarayanan, & Santos, 2006). When a monkey provided a token, the trader delivered a specified food reward (see different conditions described below). The trader then stepped away from the enclosure so that the non-trading experimenter could replenish the used token. The trader then repeated this procedure, alternating between the partner and the subject for 20 total trades. The alternation was semi-random rather than strictly back and forth, to encourage the subject to attend to all of the trades rather than being able to predict with whom the experimenter would trade. The first trader left the trading area after completing 20 trades, and the second trader moved into position to conduct 20 trades. The order of the traders was counterbalanced across days.

Training sessions allowed subjects to learn that both traders delivered identical rewards to the subject position, but that one trader provided an equal reward to the partner position whereas the other trader provided an unequal reward to the partner position. Subjects completed three training sessions before moving on to the preference-testing period. The nonsocial conditions followed an identical procedure except that the traders dropped treats into the bucket rather than trading them for tokens with the conspecific partner.

#### 2.3.3. Preference-testing sessions

During the preference-testing sessions, subjects chose between the two traders they learned about in the training sessions. At the beginning of each testing session, the subject was allowed entry into the side chamber of the testing enclosure. The social partner or nonsocial bucket was located in the previously described position, again located as previously described. Before assessing the subjects' choices between the two traders, we first presented the subjects with additional training trials. These "reminder" training trials were identical to those presented in the training period, except that the traders positioned themselves on the left and right side of the side chamber rather than at the front of the testing enclosure. Each trader completed four trades on each side of the side chamber, for a total of eight reminder trades per trader. The reminder trials served two purposes. First, they ensured that the subjects would be willing to trade with either trader and on either side of the testing chamber. Second, they ensured that the subjects remembered the specific foods that they and the partner (or bucket) received from each of the two traders. Compared to the original training trials, these reminder trials took place in strict alternation and had more distance between the subject and the partner.

Please cite this article as: Sheskin, M., et al., Capuchin monkeys (*Cebus apella*) fail to show inequality aversion in a no-cost situation, *Evolution and Human Behavior* (2013), http://dx.doi.org/10.1016/j.evolhumbehav.2013.10.004

After completing these 16 reminder trades, subjects were tested on a set of 20 preference trials. During these trials, the traders did not interact with the partner or the bucket. In each test trial, the subject received one token from the non-trading experimenter and then picked one of the two traders for an exchange. Traders began each trial on either side of testing chamber (see Fig. 2, right) with their backs to the monkey. Once the subject received a token, both traders turned around and simultaneously extended a hand to offer a trade. After one of the traders was given a token, the other trader turned away from the monkey while the chosen trader completed the trade. The traders then switched sides and waited for the subject to receive another token to begin the next trial. Each subject completed 5 days of preference-testing sessions per condition, for a total of 100 trials per subject per condition.

### 2.4. Conditions

#### 2.4.1. Basic choice condition

All subjects first completed a basic choice condition to acclimate the monkeys to our token trading procedure and to ensure that monkeys could show preferences in our set-up. This basic choice condition did not include training sessions and required high performance to "pass," ensuring that any subject who completed this condition could show preferences in our method.

Specifically, we presented the subject with test sessions in which they received 40 trials of a choice between a trader who offered grapes (the medium-value reward) to both the subject and the partner and a trader who offered cucumbers (the low-value reward) to both the subject and the partner. If monkeys understood the choice task and attended to the kinds of rewards delivered, we predicted that they should reliably choose the trader who offered the grapes rather than the one who offered cucumbers. In order to pass the basic choice condition, subjects were required to show a significant preference for trading with the experimenter that offered grapes (75% criterion across 2 days of testing, a level of preference that would far exceed the significance threshold for the other conditions). Only monkeys who succeeded in this basic choice condition were allowed to move on to the experimental condition (no monkeys were excluded).

#### 2.4.2. Experimental conditions

After completing the basic choice condition, subjects were run through each of the four experimental conditions (see Table 1) in a counterbalanced order. In the *social disadvantageous inequality* condition, the equal trader provided a grape to the subject and a grape to the partner, while the unequal trader was a Disadvantageous Trader (DT) who provided a grape to the subject and a dumpling (high-value treat) to the partner. In the *social advantageous inequality* condition, the equal trader provided a grape to the subject and a grape to the partner, while the unequal trader was an Advantageous Trader (AT) who provided a grape to the subject and a cucumber (low-value) to the partner. The two nonsocial control conditions were identical to the social test conditions, except that the partner was replaced with a bucket. During the *nonsocial disadvantageous inequality* condition, the equal trader provided a grape to the subject and placed a grape into the bucket, while the DT provided a grape to the subject and placed a dumpling (high-value) into the bucket. During the *nonsocial advantageous inequality* condition, the equal trader provided a grape to the subject and placed a grape into the bucket, while the unequal trader was an AT who provided a grape to the subject and placed a cucumber (low-value) into the bucket.

Note that in each of the above experimental conditions, subjects received grapes from every trader. Thus, it is only on the basis of *relative evaluations* with the partner (and perhaps with the bucket) that subjects would have any basis to react differently to the traders. Furthermore, because each subject saw each unique experimenter in only one condition, subjects' preferences for one individual experimenter could not transfer between conditions.

**Table 1**
The 2 × 2 design for experimental conditions.

| | Social test condition | Nonsocial control condition |
|---|---|---|
| Disadvantageous inequity | *Unequal trader*: Subject receives a lower-valued payoff (grape) than a conspecific receives (dumpling)<br>*Equal trader*: Subject receives an equal payoff (grape) to that of a conspecific (grape) | *Unequal trader*: Subject receives a lower-valued payoff (grape) than what is placed in a bucket (dumpling)<br>*Equal trader*: Subject receives an equal payoff (grape) to what is placed in a bucket (grape) |
| Advantageous inequity | *Unequal trader*: Subject receives a higher-valued payoff (grape) than a conspecific receives (cucumber)<br>*Equal trader*: Subject receives an equal payoff (grape) to that of a conspecific (grape) | *Unequal trader*: Subject receives a higher-valued payoff (grape) than what is placed in a bucket (cucumber)<br>*Equal trader*: Subject receives an equal payoff (grape) to what is placed in a bucket (grape) |

The cells depicted here describe what the "unequal" and "equal" traders did across the four different experimental conditions.

## 3. Results

In the basic choice condition, all four subjects quickly formed preferences for the trader who gave the better grape rewards, with each passing the 2-day 75% threshold after 2 or 3 days (2 days of testing: AG, 3 days of testing: JM, HG, NN). These results indicate that all of our subjects could show preferences in our setup and allowed them to continue on to the experimental conditions.

We then analyzed monkeys' performance in the experimental conditions using binomial probability estimates for each of our four monkeys across the four conditions (nonsocial versus social situations, DI versus AI), with 100 choices per monkey per condition. To correct for the use of multiple comparisons, we Bonferroni adjusted our $\alpha$ level ($\alpha = .0125$). At this alpha level, we observed no preferences in either of the nonsocial conditions (see Table 2). Three of our four monkeys showed no preferences in the social conditions. One monkey, JM, did show preferences in both of the social conditions. JM showed a reliable preference for the equal trader in the social version of the AI condition. In contrast, in the DI social condition, JM showed the opposite preference, reliably trading with the unequal Disadvantageous Trader over the equal trader.

Comparing JM's control and social conditions, we find that her performance on the DI social condition was not different from the DI control condition (Fisher's exact $2 \times 2$, $p = .46$), but was different on the AI conditions (Fisher's exact $2 \times 2$, $p < .01$). Specifically, JM preferred the equal trader over the AT *more* when the AT was giving cucumber to the partner monkey compared to when the AT was giving cucumber to a bucket.

**Table 2**
The percent of trials (out of 100) that each subject selected the equal trader in the AI and DI conditions, both social and nonsocial.

| | DI nonsocial | | AI nonsocial | | DI social | | AI social | |
|---|---|---|---|---|---|---|---|---|
| | % | *p*-Value | % | *p*-Value | % | *p*-Value | % | *p*-Value |
| AG | 46 | .24 | 54 | .24 | 51 | .46 | 44 | .14 |
| HG | 47 | .31 | 60 | .03 | 41 | .04 | 54 | .24 |
| HR | 55 | .18 | 48 | .38 | 59 | .04 | 52 | .38 |
| JM | 39 | .02 | 45 | .18 | 33 | <.01 | 69 | <.01 |

With a Bonferroni-adjusted $\alpha$-level ($\alpha = .0125$), only JM's social conditions are significantly different from chance.

Please cite this article as: Sheskin, M., et al., Capuchin monkeys (*Cebus apella*) fail to show inequality aversion in a no-cost situation, *Evolution and Human Behavior* (2013), http://dx.doi.org/10.1016/j.evolhumbehav.2013.10.004

## 4. Discussion

Despite using a no-cost preference measure that minimized competing demands on our subjects, we found little evidence that capuchins are concerned with the equality of payoffs received by themselves compared to others. Specifically, in both of the test conditions, three of the four subjects did not show any trader preferences. Regardless of whether the unequal trader had a history of giving the subject less than the partner or of giving the partner less than the subject, these three subjects did not show preferences in favor of either the equal or the unequal trader. Importantly, each of these monkeys demonstrated the appropriate preference in the qualifying "basic choice" condition, choosing the trader who had previously given the better reward to both subject and partner over the trader who gave the lesser reward to each.

One of the subjects, JM, however, did show preferences in the two test conditions (but, importantly, not in the two nonsocial control conditions). This preference was significantly different from the nonsocial control for the advantageous inequality conditions, suggesting that JM preferred the unequal trader that gave the partner a better reward than her. These results are not consistent with an equality motivation, but are consistent with either an image scoring account in which a subject might prefer to interact with an experimenter who has been shown to provide high rewards to a third party (e.g., Horowitz, 2012), or a prosocial account in which a subject might generously prefer for a conspecific to receive high rewards (e.g., Lakshminarayanan & Santos, 2008). More generally, these results suggest that capuchins might be able to form preferences about social agents based on their previous behavior. This behavior may not have been observed previously (e.g., Brosnan & de Waal, 2009) either because of the repetition needed for preference formation or because capuchins track differential rewards (as in the current study) better than failures to reward (as in Brosnan & de Waal, 2009).

Why might JM, but not the other subjects, have shown a preference for the trader who gave the partner the best possible reward? One possibility is that these results may have been influenced by the fact that the partner used in this study was the alpha male of our colony. Although it was necessary to use a high-ranking partner due to the set-up of our enclosure, previous findings provide some reason to suspect that monkeys may show weaker preferences for individuals who are prosocial toward high-ranking individuals. In a study by Takimoto, Kuroshima, and Fujita (2009), capuchin monkeys were allowed to deliver high or low payoffs to monkeys of different ranks. In contrast to their prosocial tendencies with low-ranking recipients, subjects had a tendency to provide the lower-valued payoff to the dominant monkey, which was atypical given capuchins' tendency to deliver higher-valued payoffs to others (e.g., de Waal et al., 2008; Lakshminarayanan & Santos, 2008). This result suggests that capuchins' prosocial preferences may be reduced when the partner is high ranking. Assuming that primates might show preferences for traders who provide the distribution of outcomes that the subjects would have chosen, had they been given the chance, then our use of the alpha male as partner may have worked against other monkeys showing a pattern similar to JM (who at the time of testing was the highest ranking female). Importantly, it is a very typical situation for the alpha male to receive more and better food than the other monkeys. This is true both when food is available in the cage and the alpha male monopolizes it and when humans give the alpha male high-value food in one area of the cage to distract him from food being given out to other monkeys in a different area. More individuals might show a pattern similar to JM if a lower-ranking partner were used. Either way, it is clear from our data that none of our subjects showed an aversion to receiving either more or less than another monkey, even though there was no cost for showing a preference. Furthermore, only one subject showed any significant preferences for or against any experimenters based on previous interactions with a third party. These results suggest that equality concerns and payoffs to third parties may not influence capuchins preferences for social interaction partners.

However, it should be noted that although trades were conducted in close proximity as in previous studies (e.g., Brosnan & de Waal, 2003), we could not assess the attention the subjects paid to the partner's trades due to the structure of the set-up we used. Although we specifically used our alpha male as the partner to make his payoffs more salient (e.g., see Horner, Proctor, Bonnie, Whiten, & de Waal, 2010), it is possible that our subjects did not sufficiently attend to his payoffs. Future research should measure subjects' attentiveness to their partner and his payoffs directly. In addition, the cognitive load of attending to two experimenters interactions with a partner monkey may have limited the formation of long-term preferences about the experimenters. This is consistent with the failure of Brosnan and de Waal (2009) to find preferences for a consistently rewarding experimenter over an inconsistently rewarding experimenter. If so, future research might investigate whether such a cognitive limitation is a barrier to the practical use of equality concerns for guiding a nonhuman's partner-selection behavior. Additionally, future research might increase the inequity by providing both unequal rewards and requiring unequal work: the strongest results in Brosnan and de Waal (2003) resulted from providing the partner with a higher reward *and* not requiring a token trade from the partner.

The no-cost preference method we employ here may be useful for future tests of fairness concerns in other primate species, as it avoids the inhibitory problems inherent in food-rejection methods. Specifically, future use of the no-cost preference method may reveal fairness preferences that might otherwise be obscured by inhibitory control problems, the cost of rejecting a reward, and preferences that are the reverse of experimental predictions. Furthermore, the preference measure is well suited to expand on the image scoring literature (e.g., Russell et al., 2008), in which an individual might choose partners observed providing high benefits to others. A trader-preference method can be used to investigate situations in which primates might socially evaluate others and form stable preferences for individuals based on their behaviors (e.g., to select interaction partners, Baumard et al., 2013), shedding light on which "building blocks" of human morality might be found in other species (Flack & De Waal, 2000).

## Acknowledgments

The authors would like to thank Brandon Baker, Danny Ball, Caroline Caine, James Cersonsky, Isabelle Chafkin, Clay Chiles, Vlad Chituc, Alex Chituc, Caroline Drucker, Joe Ficek, Matthew Gaba, Chris Krupenye, Adrienne Lighten, Lauren Lisann, Ellis Ludwig-Leone, Jarrett Lovelett, Ashley Malone, Tanya Mayer, Alex Milvae, Cora Mukerji, Calah Singleton, Matthew Slotkin, Jaya Wen and Huanran Zhong for their help running these studies. They also acknowledge the following organizations for their help in funding this work: the University of Chicago ARETE Science of Virtues Program, the McDonnell Scholar Award Program, and the University of Pennsylvania Positive Neuroscience Award Program. This study was approved by the Yale University Institutional Animal Care and Use Committee and conforms to the guidelines for the use of animals in research.

## References

Addessi, E., Paglieri, F., & Focaroli, V. (2011). The ecological rationality of delay tolerance: Insights from capuchin monkeys. *Cognition, 119*, 142–147.

Amici, F., Aureli, F., & Call, J. (2008). Fission-fusion dynamics, behavioral flexibility, and inhibitory control in primates. *Current Biology: CB, 18*(18), 1415–1419.

Anderson, J. R., Kuroshima, H., & Fujita, K. (2010). Delay of gratification in capuchin monkeys (*Cebus apella*) and squirrel monkeys (*Saimiri sciureus*). *Journal of Comparative Psychology, 124*, 205–210.

Baumard, N., André, J. B., & Sperber, D. (2013). A mutualistic approach to morality: The evolution of fairness by partner choice. *The Behavioral and Brain Sciences, 36*(1), 59–78.

Please cite this article as: Sheskin, M., et al., Capuchin monkeys (*Cebus apella*) fail to show inequality aversion in a no-cost situation, *Evolution and Human Behavior* (2013), http://dx.doi.org/10.1016/j.evolhumbehav.2013.10.004

Beran, M. J., Evans, T. A., Paglieri, F., McIntyre, J. M., Addessi, E. & Hopkins, W. D. (in press). Chimpanzees (Pan troglodytes) can wait, when they choose to: a study with the hybrid delay task. *Animal Cognition*, [Epub ahead of print].

Birch, L. L., & Billman, J. (1986). Preschool children's food sharing with friends and acquaintances. *Child Development*, *57*, 387–395.

Blake, P. R., & McAuliffe, K. (2011). "I had so much it didn't seem fair": Eight-year-olds reject two forms of inequality. *Cognition*, *120*, 215–224.

Boysen, S. T., & Berntson, G. G. (1995). Responses to quantity: Perceptual versus cognitive mechanisms in chimpanzees *Pan troglodytes*. *Journal of Experimental Psychology: Animal Behavior Processes*, *21*, 82–86.

Bräuer, J., Call, J., & Tomasello, M. (2006). Are apes really inequity averse? *Proceedings. Biological Sciences/the Royal Society*, *273*(1605), 3123–3128.

Bräuer, J., Call, J., & Tomasello, M. (2009). Are apes inequality averse? New data on the token-exchange paradigm. *American Journal of Primatology*, *71*, 175–181.

Brosnan, S. F. (2006). Nonhuman species' reactions to inequality and their implications for fairness. *Social Justice Research*, *19*, 153–185.

Brosnan, S. F. (2008). Responses to inequality in non-human primates. In P. W. Glimcher, C. Camerer, E. Fehr, & R. Poldrack (Eds.), *Neuroeconomics: Decision making and the brain* (pp. 285–302). Amsterdam: Elsevier.

Brosnan, S. F., & de Waal, F. B. M. (2003). Monkeys reject unequal pay. *Nature*, *425*, 297–299.

Brosnan, S. F., & de Waal, F. B. M. (2004). Reply to "inequity aversion in capuchins". *Nature*, *428*, 140.

Brosnan, S. F., & de Waal, F. B. M. (2006). Partial support from a non-replication: Comment on Roma, Silberberg, Ruggiero, and Suomi (2006). *Journal of Comparative Psychology*, *120*, 74–75.

Brosnan, S. F., & de Waal, F. B. M. (2009). *Cebus apella* tolerate intermittent unreliability in human experimenters. *International Journal of Primatology*, *30*(5), 663–674.

Brosnan, S. F., Houser, D., Leimgruber, K., Xiao, E., Chen, T., & de Waal, F. B. M. (2010a). Competing demands of prosociality and equity in monkeys. *Evolution and Human Behavior*, *31*, 279–288.

Brosnan, S. F., Schiff, H. C., & de Waal, F. B. M. (2005). Tolerance for inequality may increase with social closeness in chimpanzees. *Proceedings of the Royal Society B*, *272*, 253–258.

Brosnan, S. F., Talbot, C., Ahlgren, M., Lambeth, S. P., & Schapiro, S. J. (2010b). Mechanisms underlying responses to inequitable outcomes in chimpanzees, *Pan troglodytes*. *Animal Behavior*, *79*, 1229–1237.

Burkart, J. M., Fehr, E., Efferson, C., & van Schaik, C. P. (2007). Other-regarding preferences in a non-human primate: Common marmosets provision food altruistically. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(50), 19762–19766.

Camerer, C., & Foundation, R. S. (2003). *Behavioral game theory: Experiments in strategic interaction*. Princeton, NJ: Princeton University Press.

Chen, M. K., Lakshminarayanan, V., & Santos, L. R. (2006). How basic are behavioral biases? Evidence from capuchin monkey trading behavior. *Journal Political Economy*, *114*, 517–537.

Chen, M. K., & Santos, L. R. (2006). Some thoughts on the adaptive function of inequality aversion: An alternative to Brosnan's social hypothesis. *Social Justice Research*, *19*, 201–207.

Cronin, K. A., Schroeder, K. K., Rothwell, E. S., Silk, J. B., & Snowdon, C. T. (2009). Cooperatively breeding cottontop tamarins (*Saguinus oedipus*) do not donate rewards to their long-term mates. *Journal of Comparative Psychology*, *123*, 231–241.

de Waal, F. B. M., Leimgruber, K., & Greenberg, A. R. (2008). Giving is self-rewarding for monkeys. *PNAS*, *105*, 13685–13689.

Diamond, A., & Goldman-Rakic, P. S. (1989). Comparison of human infants and rhesus monkeys on piaget's AB task: Evidence for dependence on dorsolateral prefrontal cortex. *Experimental Brain Research*, *74*, 24–40.

Dindo, M., & de Waal, F. B. M. (2007). Partner effects on food consumption in brown capuchin monkeys. *American Journal of Primatology*, *69*, 448–456.

Dubreuil, D., Gentile, M. S., & Visalberghi, E. (2006). Are capuchin monkeys (*Cebus apella*) inequality averse? *Proceedings of the Royal Society B*, *273*, 1223–1228.

Dufour, V., Pelé, M., Sterck, E. H., & Thierry, B. (2007). Chimpanzee (*Pan troglodytes*) anticipation of food return: Coping with waiting time in an exchange task. *Journal of Comparative Psychology*, *121*, 145–155.

Evans, T. A., Beran, M. J., Paglieri, F., & Addessi, E. (2012). Delaying gratification for food and tokens in capuchin monkeys (*Cebus apella*) and chimpanzees (*Pan troglodytes*): When quantity is salient, symbolic stimuli do not improve performance. *Animal Cognition*, *15*, 539–548.

Fehr, E., Bernhard, H., & Rockenbach, B. (2008). Egalitarianism in young children. *Nature*, *454*, 1079–1083.

Fehr, E., & Schmidt, K. M. (1999). A theory of fairness, competition, and cooperation. *Quarterly Journal Economics*, *114*, 817–868.

Flack, J. C., & De Waal, F. B. M. (2000). Any animal whatever. Darwinian building blocks of morality in monkeys and apes. *Journal of Consciousness Studies*, *7*, *1*(2), 1–29.

Fletcher, G. E. (2008). Attending to the outcome of others: Disadvantageous inequity aversion in male capuchin monkeys (*Cebus apella*). *American Journal of Primatology*, *70*(9), 901–905.

Gerson, R. P., & Damon, W. (1978). Moral understanding and children's conduct. *New Directions for Child and Adolescent Development*, *2*, 41–59.

Guth, W., Schmittberger, R., & Schwarze, B. (1982). An experimental analysis of ultimatum bargaining. *Journal of Economic Behavior and Organization*, *3*, 367–388.

Haidt, J., & Joseph, C. (2004). Intuitive ethics: How innately prepared intuitions generate culturally variable virtues. *Daedalus*, *133*, 55–66.

Haidt, J., & Joseph, C. (2007). The moral mind: How five sets of innate intuitions guide the development of many culture-specific virtues, and perhaps even modules. In P. Carruthers, S. Laurence, & S. Stich (Eds.), *The Innate Mind. Vol. 3*. (pp. 367–391). New York, NY: Oxford University Press.

Henrich, J. (2004). Inequity aversion in capuchins? *Nature*, *428*, 139.

Henrich, J., Boyd, R., Bowles, S., Gintis, H., Fehr, E., Camerer, C., et al. (2005). 'Economic Man' in cross-cultural perspective: Ethnography and experiments from 15 small-scale societies. *Behavioral and Brain Sciences*, *28*, 795–855.

Henrich, J., Ensimger, J., McElreath, R., Barr, A., Barrett, C., Bolyanatz, A., et al. (2010). Markets, religion, community size, and the evolution of fairness and punishment. *Science*, *327*, 1480–1484.

Henrich, J., McElreath, R., Barr, A., Ensminger, J., Barrett, C., Bolyanatz, A., et al. (2006). Costly punishment across human societies. *Science*, *312*, 1767–1770.

Herrmann, E., Keupp, S., Hare, B., Vaish, A., & Tomasello, M. (2012). Direct and indirect reputation formation in nonhuman great apes (*Pan paniscus*, *Pan troglodytes*, *Gorilla gorilla*, *Pongo pygmaeus*) and human children (*Homo sapiens*). *Journal of Comparative Psychology*, *127*, 63–75.

Hopper, L. M., Lambeth, S. P., Schapiro, S. J., Bernacky, B. J., & Brosnan, S. F. (2013). The ontogeny of social comparisons in rhesus macaques (*Macaca mulatta*). *Journal of Primatology*, *02*, 109.

Horner, V., Carter, J. D., Suchak, M., & de Waal, F. B. (2011). *Spontaneous prosocial choice by chimpanzees*. : Proceedings of the National Academy of Sciences of the United States of America.

Horner, V., Proctor, D., Bonnie, K. E., Whiten, A., & de Waal, F. B. M. (2010). Prestige affects cultural learning in chimpanzees. *PLoS One*, *5*, e10625.

Horowitz, A. (2012). Fair is fine, but more is better: Limits to inequity aversion in the domestic dog. *Social Justice Research*, *25*(2), 195–212.

Jensen, K., Call, J., & Tomasello, M. (2007). Chimpanzees are rational maximizers in an ultimatum game. *Science*, *318*, 107–109.

Jensen, K., Call, J., & Tomasello, M. (2013). Chimpanzee responders still behave like rational maximizers. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(20), E1837.

Kahneman, D., Knetsch, J. L., & Thaler, R. (1986). Fairness as a constraint on profit seeking: Entitlements in the market. *The American Economics Review*, *76*, 728–741.

Lakshminarayanan, V. R., & Santos, L. R. (2008). Capuchin monkeys are sensitive to others' welfare. *Current Biology*, *18*, R999–R1000.

LoBue, V., Nishida, T., Chiong, C., DeLoache, J. S., & Haidt, J. (2009). When getting something good is bad: Even three-year-olds react to inequality. *Social Development*, *20*, 154–170.

Marshall-Pescini, S., Passalacqua, C., Ferrario, A., Valsecchi, P., & Prato-Previde, E. (2011). Social eavesdropping in the domestic dog. *Animal Behaviour*, *81*(6), 1177–1183.

Massen, J. J., Van Den Berg, L. M., Spruijt, B. M., & Sterck, E. H. (2012). Inequity aversion in relation to effort and relationship quality in long-tailed macaques (*Macaca fascicularis*). *American Journal of Primatology*, *74*(2), 145–156.

Melis, A. P., Warneken, F., Jensen, K., Schneider, A. C., Call, J., & Tomasello, M. (2011). Chimpanzees help conspecifics obtain food and non-food items. *Proceedings of the Royal Society B*, *278*, 1405–1413.

Neiworth, J. J., Johnson, E. T., Whillock, K., Greenberg, J., & Brown, V. (2009). Is a sense of inequity an ancestral primate trait? Testing social inequity in cotton top tamarins (*Saguinus oedipus*). *Journal of Comparative Psychology*, *123*, 10–17.

Olson, K. R., & Spelke, E. S. (2008). Foundations of cooperation in young children. *Cognition*, *108*, 222–231.

Paukner, A., Suomi, S. J., Visalberghi, E., & Ferrari, P. F. (2009). Capuchin monkeys display affiliation toward humans who imitate them. *Science*, *325*, 880–883.

Pelé, M., Micheletta, J., Uhlrich, P., Thierry, B., & Dufour, V. (2011). Delay maintenance in tonkean macaques (*Macaca tonkeana*) and brown capuchin monkeys (*Cebus apella*). *International Journal of Primatology*, *32*, 149–166.

Proctor, D., Williamson, R. A., de Waal, F. B. M., & Brosnan, S. F. (2013a). Chimpanzees play the ultimatum game. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(6), 2070–2075.

Proctor, D., Williamson, R. A., de Waal, F. B. M., & Brosnan, S. F. (2013b). Reply to Jensen et al.: Equitable offers are not rationally maximizing. *Proceedings of the National Academy of Sciences*, *110*(20), E1838.

Range, F., Horn, L., Viranyi, Z., & Huber, L. (2009). The absence of reward induces inequity aversion in dogs. *Proceedings of the National Academy of Sciences*, *106*(1), 340–345.

Range, F., Leitner, K., & Virányi, Z. (2012). The influence of the relationship and motivation on inequity aversion in dogs. *Social Justice Research*, *25*(2), 170–194.

Roma, P. G., Silberberg, A., Ruggiero, A. M., & Suomi, S. J. (2006). Capuchin monkeys, inequity aversion, and the frustration effect. *Journal Comparative Psychology*, *120*, 67–73.

Rosati, A. G., Stevens, J. R., Hare, B., & Hauser, M. D. (2007). The evolutionary origins of human patience: Temporal preferences in chimpanzees, bonobos, and human adults. *Current Biology : CB*, *17*(19), 1663–1668.

Russell, Y. I., Call, J., & Dunbar, R. I. (2008). Image scoring in great apes. *Behavioural Processes*, *78*(1), 108–111.

Shaw, A., & Olson, K. R. (2012). Children discard a resource to avoid inequity. *Journal of Experimental Psychology: General*, *141*, 382–395.

Sigelman, C. K., & Waitzman, K. A. (1991). The development of distributive justice orientations: Contextual influences on children's resource allocations. *Child Development*, *62*, 1367–1378.

Silberberg, A., Crescimbene, L., Addessi, E., Anderson, J. R., & Visalberghi, E. (2009). Does inequality aversion depend on a frustration effect? A test with capuchin monkeys (*Cebus apella*). *Animal Cognition*, *12*, 505–509.

Silk, J. B., Brosnan, S. F., Vonk, J., Henrich, J., Povinelli, D. J., Richardson, A. S., et al. (2005). Chimpanzees are indifferent to the welfare of unrelated group members. *Nature*, *437*(7063), 1357–1359.

Stevens, J. R., Rosati, A. G., Heilbronner, S. R., & Mühlhoff, N. (2011). Waiting for grapes: Expectancy and delayed gratification in bonobos. *International Journal of Comparative Psychology*, *24*, 99–111.


Please cite this article as: Sheskin, M., et al., Capuchin monkeys (*Cebus apella*) fail to show inequality aversion in a no-cost situation, *Evolution and Human Behavior* (2013), http://dx.doi.org/10.1016/j.evolhumbehav.2013.10.004

Subiaul, F., Vonk, J., Okamoto-Barth, S., & Barth, J. (2008). Do chimpanzees learn reputation by observation? Evidence from direct and indirect experience with generous and selfish strangers. *Animal Cognition*, *11*(4), 611–623.

Takimoto, A., Kuroshima, H., & Fujita, K. (2009). Capuchin monkeys (*Cebus apella*) are sensitive to others' reward: An experimental analysis of food-choice for conspecifics. *Animal Cognition*, *13*, 249–261.

Tinklepaugh, O. L. (1928). An experimental study of representative factors in monkeys. *Journal Comparative Psychology*, *8*, 197–236.

Tricomi, E., Rangel, A., Camerer, C. F., & O'Doherty, J. P. (2010). Neural evidence for inequality-averse social preferences. *Nature*, *463*, 1089–1091.

Wascher, C. A., & Bugnyar, T. (2013). Behavioral responses to inequity in reward distribution and working effort in crows and ravens. *PloS One*, *8*(2), e56885.

Wright, N. D., Hodgson, K., Fleming, S. M., Symmonds, M., Guitart-Masip, M., & Dolan, R. J. (2012). Human responses to unfairness with primary rewards and their biological limits. *Scientific Reports*, *2*, 593.

Zaki, J., & Mitchell, J. P. (2011). Equitable decision making is associated with neural markers of intrinsic value. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(49), 19761–19766.

Zizzo, D. J., & Oswald, A. J. (2001). Are people willing to pay to reduce others' incomes? *Social Interactions and Economic Behavior*, *63–64*, 39–62.

Please cite this article as: Sheskin, M., et al., Capuchin monkeys (*Cebus apella*) fail to show inequality aversion in a no-cost situation, *Evolution and Human Behavior* (2013), http://dx.doi.org/10.1016/j.evolhumbehav.2013.10.004