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Squirrel monkeys' response to inequitable outcomes indicates a behavioural convergence within the primates

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SUMMARY

Although several primates respond negatively to inequity, it is unknown whether this results from homology or convergent processes. Behaviours shared within a taxonomic group are often assumed to be homologous, yet this distinction is important for a better understanding of the function of the behaviour. Previous hypotheses have linked cooperation and inequity responses. Supporting this, all species in which inequity responses have been documented are cooperative. In this study, we tested this hypothesis by investigating the response to inequity in squirrel monkeys, which share a phylogenetic Family with capuchin monkeys, but do not cooperate extensively. Subjects exchanged tokens to receive food rewards in conditions in which the level of effort required and reward received varied. Squirrel monkeys did not respond negatively to inequity. However, the monkeys were sensitive to the variation present in the task; male subjects showed a contrast effect and, as in previous studies, subjects were more sensitive to differences in reward in the context of a task than when rewards were given for free. Taken with other results, these results support the hypothesis that a negative response to inequity evolved convergently in primates, probably as a mechanism for evaluating outcomes relative to one's partners in cooperative species.

1. INTRODUCTION

Several species are known to respond negatively to inequitable outcomes (*Cebus apella:* [1-3]; *Pan troglodytes*: [4, 5]; *Canus domesticus*: [6]). In these studies, subjects refused both participation and food rewards when they received a lower-value reward than their partner. This cannot be explained by individual contrast, as subjects were willing to accept lower-value rewards than an initial offer as long as the partner received the same, lower-value, food. Thus, this behaviour is best described as a social contrast, in which subjects form expectations about their outcomes based on the outcomes of others.

What is unknown is the function of the behaviour. One hypothesis is that negative reactions to unequal reward distributions evolved as a mechanism to promote long-term cooperation [7, 8]. This hypothesis is supported by several indirect lines of evidence. First, the response occurs only in the context of a task [5], possibly indicating that joint efforts lead to expectations of joint payoffs [3]. Second, inequitable outcomes can stall cooperation, even when both individuals would receive an absolute gain [9].

However, this hypothesis has not been tested, as all the species in which an inequity response has been detected, including humans, frequently cooperate (e.g. increase their fitness by working together; [10]) outside of kin or mating relationships. Chimpanzee males cooperatively hunt and defend their territory [11]. Capuchins coordinate many activities [12], possibly including hunting [13]. Both of these species and bonobos, which also show a tendency to respond to inequity [14], cooperate extensively in the lab [15-17]. Canines, too, display many of these characteristics [18].

Thus, the purpose of this study is to test the hypothesis that inequity is a convergent trait linked to cooperation by investigating the response to inequity in the

squirrel monkey, a highly social primate not known to cooperate. While females occasionally form coalitions [19] and males may work together for olfactory investigations of female genitalia [20], explicit cooperation is not documented in the wild or captivity. Food sharing, a measure of tolerance linked to cooperation [15], occurs only under harassment [21], unlike capuchins, who share spontaneously [22]. Squirrel monkeys also share a phylogenetic Family (Cebidae) with capuchins, and such close phylogenetic relationships provide the best comparison. We used the same paradigm as previous tests with capuchins and chimpanzees [1, 5]. Thus, these results help determine whether inequity responses are due to homology or convergence related to cooperation.

2. MATERIALS AND METHODS

Twenty-four adult squirrel monkeys (*Saimiri sciureus and S. boliviensis*; 14 males and 10 females) were tested in their home cages at the Keeling Center for Comparative Medicine and Research of the UTMD Anderson Cancer Center, Bastrop, TX, USA. Prior to testing, food preferences were determined using a dichotomous-choice test to establish a high-value reward (HVR) and a medium-value reward (MVR; [23]). Subjects had to prefer the HVR to the MVR at least 80% of the time in two sessions on different days and, in a separate session, eat 10 consecutive pieces of the MVR.

Subjects participated in two sessions of four conditions in the subject role: inequity baseline (IB), equity control (EC), individual contrast (IC), and gift reward (GR). The order of sessions was randomized for each pair. Each test session included 30 trials alternating between the partner and the subject so that each individual completed 15 trials per test session. For more details, see ESM.

To test whether the squirrel monkeys responded when the other received a different reward (either a higher-valued or a lower-valued reward), we compared subjects' reactions in the IB to the EC. In the IB, both monkeys had to exchange; however, the subject received a MVR and the partner received a HVR. In the EC, both monkeys exchanged for an MVR. To determine whether the subjects' response was due to the partner getting a better reward (social contrast) or frustration over not receiving a better reward that

appeared to be available (IC), we compared the IB to the IC, in which both monkeys were shown a HVR prior to exchange, but after completing the exchange received a MVR. To test the hypothesis that the inclusion of a task elicits a different response, we compared the IB to the GR, in which both individuals received their respective reward (subject MVR, partner HVR) for 'free', without having to exchange a token beforehand.

All comparisons used the overall refusal rate (combining refusal to participate with refusals of the reward). Overall comparisons were done with Friedman's Tests, and paired comparisons with Wilcoxon Sign-Rank exact tests (analyses were repeated with repeated measures ANOVAs to take in to account possible nesting, despite the marginal sample size for parametric tests; see ESM). One-fifth (20%) of the data were re-coded from video tapes by coders blind to the hypotheses. Coders showed high agreement on the monkeys' refusal rate (agreed on 99.8% of trials, Cohen's κ=0.995).

3. RESULTS & DISCUSSION

Squirrel monkeys varied in their rate of refusal among the four conditions (figure 1, see also figure S1; Friedman's Test, n=24, χ^2=32.309, df=3, p<0.001). However, they did not respond differently when their partner got a better reward as compared to when both got the same, lower-value outcome (comparing IB to EC: T+=137, n=22, p=0.733). Thus, these monkeys showed no evidence of social contrast, or inequity. On the other hand, the monkeys did respond differently when they were offered a HVR but then received a lower one, again as compared to when they were given the same lower-value reward (comparing IC to EC: T+=202, n=23, p=0.051), indicating individual contrast. However, this behaviour was clearly driven by the males' response (see below). In a direct comparison, they were more responsive to individual than social contrast (comparing IB to IC: T+=50.5, n=21, p=0.023).

Previous results have found sex differences in responses [5], thus we also analyzed males and females separately. Neither males nor females refused more often in the IB than the EC condition (comparing IB to EC; Males: T+=49.5, n=23, p=0.779; Females: T+=9, n=5, p=0.686). However, males did refuse more often in the IC condition than the EC condition (comparing IC to EC: T+=74.5, n=13, p=0.042), while females did not (T+=6, n=6, p=0.344). Directly comparing the IC and IB (social contrast) conditions, again, males were more responsive to individual than to social contrast whereas females were indifferent (comparing IC to IB; Males: T+=6, n=11, p=0.016; Females: T+=14.5, n=6, p=0.395). Thus male squirrel monkeys, but not females, compare their outcomes to those which were offered previously.

Considering the role of effort, Brosnan [8] hypothesized that individuals would show stronger reactions when a task was present than when rewards were given for free, but only one within-subject test has verified this (among chimpanzees: [5]; see also [24] for a between-subjects comparison in tamarins). We find that overall, despite not responding to inequity, squirrel monkeys refused less often when rewards were given for free than when they had to exchange to obtain those rewards, although this response appears to be due mainly to the males' behaviour (overall: IB vs GR: T+=283, n=24, p<0.001; Males: T+=102, n=14, p=0.002; Females: T+=18, n=6, p=0.115; see Figure S3). One possible explanation is that this is due to feeding practices in captive groups, which may result in food being distributed unequally (e.g. resulting from dominance interactions and scramble competition; [5]). However, subjects may also treat earned rewards and 'free' rewards differently [25], including expecting outcomes following joint efforts to be more equal than those resulting from good fortune [5,3].

Thus, we find that, unlike more cooperative species, squirrel monkeys do not respond to social contrast, that is, they do not refuse interactions if their partner receives a better reward for the same task. There are several possible explanations for the difference in outcomes between squirrel and capuchin monkeys. First, it is possible that this trait is ancestral among primates, but was lost in squirrel monkeys. However, other studies find no evidence of inequity in orangutans [14, 26, 27], and little evidence in tamarins [24]. A second possibility is that the response is an emergent property of advanced cognition, seen primarily in species such as capuchins and chimpanzees, with high brain-to-body ratios [28]. Again, however, the lack of a response in orangutans suggests that this is not the case. The response could also be affected by social organization, with more gregarious species evolving greater responses to social contrast, a hypothesis which is not supported by either the orangutan or squirrel monkey data. Thus, the current data suggest that the response to inequity is the result of convergent processes, rather than homology, and, at present, best support the hypothesis that cooperation and the negative response to inequity emerged in tandem.

Of course, these data do not indicate a causal relationship. One hypothesis is that following the emergence of cooperation, there was increased selective pressure on the ability to determine when one's cooperative relationships were no longer beneficial. A plausible mechanism is that individuals who reacted when their outcomes differed from those of one's partners were more likely to find new social partners [8, 29]. Functionally, this may result in better (i.e., more equitable) outcomes over the long term. If more equitable outcomes are also relatively better (in comparison to others' outcomes), then the behaviour would be under positive selection.

Despite the close phylogenetic relationship, a negative response to inequity in primates appears in capuchin, but not squirrel, monkeys. Thus, this appears to be a convergent trait in primates, most likely correlated with cooperation amongst non-kin and individuals who are not pairbonded. In the future, this comparative approach should be used more extensively to help us understand the context in which this and other behaviours evolved and further assist in testing hypotheses related to a behaviour's function.

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Figure 1. Mean percentage ± SEM of total refusals (token and food refusals combined) in each condition male and female subjects (see Table S1 for details of each condition). Bars indicate significant pairwise comparisons for males.

ELECTRONIC SUPPLEMENTARY MATERIAL

Subjects

Twenty-four socially-housed adult (1 to 16 years of age) squirrel monkeys (*Saimiri sciureus and S. boliviensis*; 14 males and 10 females) were tested in their home cages at the Keeling Center for Comparative Medicine and Research of the UTMD Anderson Cancer Center, Bastrop, TX, USA. None of the subjects had been previously exposed to social inequity or cooperative research situations. All subjects had *ad libitum* access to primate chow and water. At no time were the subjects ever food or water deprived. Subjects were supplemented daily with fruit or vegetable food enrichment.

Food Preference Tests

Rewards were determined prior to testing through a series of dichotomous choice tests for a variety of different fruits, vegetables, and insects (after Brosnan and de Waal 2004). Each session consisted of 10 consecutive trials in which the experimenter held up a HVR in the palm of one hand and a MVR in the other, approximately 15 cm apart, centered on the squirrel monkey. Initially, the experimenter displayed the rewards out of reach to the subject for five seconds, approximately 30 cm from the mesh. Subsequently, the experimenter simultaneously moved both hands forward to about 15 cm from the mesh so that the rewards were within the reach of the subjects. Subjects indicated their choice by reaching their hand through the mesh and taking the preferred food. To control for any side biases, presentation of the rewards alternated each trial between left and right. Subjects completed two food preference sessions on different days. Reward pairs were chosen if subjects preferred the HVR to the MVR at least 80% of the time and, in a

separate session, were willing to consume 10 pieces of the medium value food when no other food was available. Due to differences in individual preferences, different pairs of monkeys utilized different foods. However, rewards were always the same for both individuals within a pair. For four of the twelve pairs, the HVR was one quarter of a seedless grape and the MVR was a slice of almond. For two pairs, the HVR was a single meal worm and the MVR was one quarter of a grape. For another two pairs, the HVR was one quarter of a grape and the MVR was a honey-nut cheerio. For another two pairs, the HVR was a half of a raisin and the MVR was a piece of apricot. For one pair, the HVR was one quarter of a grape and the MVR was a small piece of granola. For the last pair, the HVR was one third of a marshmallow and the MVR was one quarter of a grape.

Training

Prior to testing, all subjects were trained to barter an inedible token in exchange for a food reward. Tokens consisted of polyvinyl chloride pipe 7.6 cm in length and 0.6 cm in diameter. For an exchange interaction, the experimenter showed the token to the squirrel monkey, and then gave the monkey the token. To complete the exchange, the monkey was required to place the token into a basket positioned inside the cage. The basket was placed inside the cage and used exclusively for training and testing (the basket was removed when testing was not occurring). The task was considered complete when the token hit the bottom of the basket. Upon completion of this task, the monkey was given a reward. Subjects were considered proficient at the task when they returned at least 8 out of 10 tokens in each of two sessions conducted on different days.

Testing

Pairs were removed from their social group and housed together in a room with other squirrel monkeys for the testing period. Subjects could easily observe what the other individual was exchanging and which reward they received during these interactions. Both reward containers (one for the medium value food and one for the high value food) were always present, full, and in the same position, regardless of whether they were used in the session, so that the presence of either of these rewards did not cue the subject or create differences in reaction. Responses were immediately recorded on data sheets by the experimenter and all test sessions were videotaped for later analysis and coding.

Each test session included 30 trials alternating between the partner and the subject so that each individual completed 15 trials per test sessions. The partner always exchanged prior to the subject. Time between trials was approximately 5 seconds, which was the amount of time it took the experimenter to record the results and prepare for the next trail. In each trial, the monkey had up to 10 seconds to accept the token and up to an additional 30 seconds to complete the task. After a successful trial, the experimenter lifted the correct reward from the container, placed it in the palm of their hand, raised it up in the front of the monkey (but out of reach) so that it was visible to both monkeys, and then gave the reward to the monkey who had just completed the task. Subjects could refuse to complete the task or refuse to accept the food reward. Sharing the token with a partner (pushing the token through the dividing mesh), pushing the token out of the cage (rejecting), or placing the token down inside the cage and ignoring the token, were considered refusal to complete the task. Refusals to accept the reward consisted of

sharing it with their partner, ignoring it, throwing it away, or refusing to accept it (see Table S2).

Statistics

Statistics included non-parametric repeated measures tests (Friedman's tests for overall comparisons and Wilcoxon signed ranks tests for paired comparisons). However despite the small sample size, we also ran parametric statistics (ANOVA), which allowed us to evaluate potential effects of a nested design. Parametric results are reported here. All statistics are two-tailed, and significance is considered $p<0.05$. Note that for the Wilcoxon tests, sample sizes (n) may differ due to ties, which are not included in the computation of the final test statistic.

SUPPLEMENTAL DATA

Types of Refusals

There was variation among the types of refusals for both tokens (Friedman's Test, n=24, $\chi^2 = 49.995$, df =3, $p<0.001$) and food (Friedman's Test, n=24, $\chi^2 = 22.695$, df =3, $p<0.001$; see Table S1 for complete list of refusals). Subjects were more likely to refuse the token rather than the food (Wilcoxon Sign Rank test, T+=292, n=24, $p<0.001$). In both food and token refusals, *ignore* was the most common method of refusal (65% of token refusals, 43% of food refusals), so we repeated the analyses presented in the paper (which utilized total refusals) using only ignores. This analysis yielded similar results to those based on the combined refusal rate. Monkeys varied in their ignore refusal rate among the four conditions (Figure S1; Friedman's Test, n=24, $\chi^2 = 36.214$, df =3, *p*

<0.001). They did not respond differently when their partner got a better reward as compared to when both got the same, lower-value outcome (comparing IB to EC: T+=140.5, n=23, *p*=0.939). As with total refusals, they responded differently to the individual contrast, in which they were offered a high-value reward, but received a lower value reward after returning the token (comparing IC to EC: T+=219.5, n=23, *p*=0.013). Again, in a direct comparison between individual and social contrast, the monkeys exhibited a stronger reaction to the individual than to the social contrast condition (IB to IC: T+=35, n=21, *p* =0.005). Finally, the monkeys were again less likely to respond when the rewards were handed to them for free than when they had to exchange to get those rewards (IB vs GR: T+=249, n=22, *p*<0.001).

Latency to refuse

We measured the speed with which subjects returned the token to the human experimenter (latency) as the time from which the monkey accepted the token until it was placed in to the basket. Latency did not vary among the conditions (this analysis includes only 3 conditions, because there was no task in the GR condition; Friedman's test: χ^2 =1.583, df =2, p =0.453).

Effect of a Task

Using the overall refusal data (as in the main body of the text) as well as the total ignore data, we compared the GR to the IC (Overall refusals: T+=12, n=23, *p*<0.001; ignore refusals: T+=1, n=22, p<0.001). Finally, we compared the GR to the EC (Overall refusals: T+=4.5, n=21, p<.001; ignore refusals: T+=0, n=20, p0<.001). Therefore,

regardless of the condition, the monkeys were significantly more likely to respond when a task was involved compared to when the rewards were simply handed out for 'free'.

Parametric Analyses

We repeated the nonparametric analyses on the overall refusal data (in the main body of the text) using repeated measures ANOVA to account for the possibility that nesting of subjects may have affected our results. Mauchly's test indicated that the variances of the differences between conditions were not significantly different, therefore the assumption of sphericity was not violated (χ^2 (5)= 5.027, p=0.413).

As with the Friedman's test, we find a significant effect of condition (F(3, 66)= 14.92, p<0.001). Bonferroni corrected post hoc tests showed that the squirrel monkeys did not respond differently social contrast, or inequity, as compared to the equity control, confirming our results in the main analysis (comparing IB to EC: p=1.00). However, we also found some differences using the parametric statistics. First, using this approach, the monkeys did not respond differently when they were offered a higher-value reward but then received a lower one, as compared to when they were given the same lower-value reward, indicating no individual contrast effect (comparing IC to EC: p=0.35). Moreover, in direct comparison between social and individual contrast, the monkeys did not respond differently (comparing IB to IC: p=0.228).

We also examined the role of effort through the Gift Reward condition in which no task was required. Again, we found that squirrel monkeys refused less often when rewards were given for free than when they had to exchange to obtain those rewards (comparing GR to IB: p=0.001; comparing GR to EC: p=0.002; comparing GR to IC:

$p<0.001$). Finally, while there was a significant condition X gender interaction effect ($F(3,66)=3.156$, $p=0.03$), indicating that the responses across conditions significantly differed in males and females, there was a non-significant trend for a sex difference in responses ($F(1,22)= 3.677$, $p=0.068$).

SUPPLEMENTAL DISCUSSION

One finding in this paper as well as in others (Neiworth et al. 2009) is that even in cases in which subjects do not respond negatively to inequity, there appear to be greater refusals for lesser-valued rewards in cases in which the subject must work for the reward (e.g. an exchange) as compared to cases in which a subject gets the reward for free. This mirrors the finding that individuals who do respond negatively to inequity only do so in the context of a task (e.g. Brosnan et al. 2010). Despite this consistency, it seems surprising that the task would make a difference in the case in which no inequity response is seen.

One possible explanation is that subjects in general may value objects that they work for differently than those that they receive for free (Carder and Berkowitz 1970). If this is the case, then it is clear that the effect of work is distinct from any effect of inequity. This is related to previous arguments that have been made for species which do respond negatively to inequity (e.g. Brosnan et al. 2010; van Wolkenten et al. 2007). This hypothesis posits that joint efforts elicit an expectation of joint outcomes, and so in situations in which efforts are similar, outcomes are expected to be similar, while in cases with no effort, there is no such expectation. This latter situation might be perceived as ‘good fortune’ and treated differently.

Another possibility, discussed previously (Brosnan et al. 2010) is that subjects are accustomed to receiving rewards in the context of general husbandry which are not distributed equally (dominant individuals receive more of these rewards). It is possible that simply handing rewards to individuals evokes this context, and the accompanying habituation to inequity. This may be the case even in subjects which do not appear to show responses to inequity when rewards are unequal between individuals on a task.

Figure S1. Mean percentage ± SEM of total ignores (ignore token and ignore food combined) in each condition. (see Table S1 for details of each condition). * Indicates significant pairwise comparisons between the Individual Contrast condition and the Inequity Baseline condition as well as the Equity Control condition. ** Indicates significant pairwise comparisons between the Gift Reward condition and all other conditions (Inequity Baseline, Equity Control, and Individual Contrast).

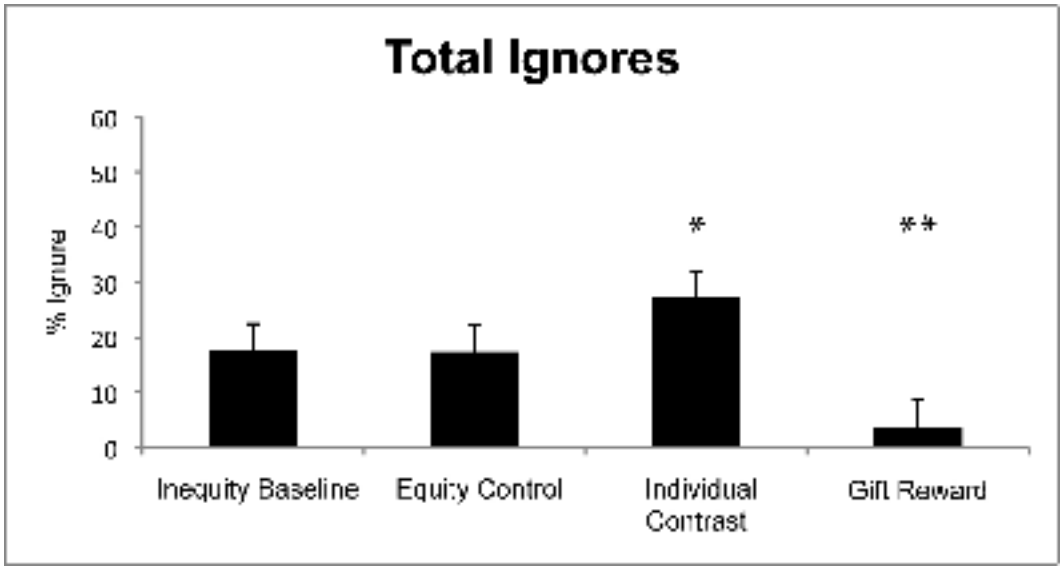

Table S1. Description of experimental conditions

Abbreviation	**Condition Name**	**Exchange**	**Food**	**Description**
IB	Inequity baseline	Both exchange	Subject medium value Partner high value	Partner exchanges for high value reward and subject exchanges for medium value reward.
EC	Equity control	Both exchange	Both receive medium value following exchange	Both subject and partner exchanged for medium value reward.

IC	Individual contrast	Both exchange	Both see high value before exchange, receive medium value following exchange	Prior to exchange, high value reward is held in front of exchanger and then is placed back in container. After successful completion of exchange, exchanger receives medium value reward.
GR	Gift reward	No exchange	Subject medium value Partner high value	Partner is given a high value reward for 'free' (e.g. without exchange) and then subject is given a medium value reward.

Behavior	**Token Variables**	**Reward Variables**
Refuse	Does not accept token w/in 10 seconds	Does not accept food w/in 5 seconds
Ignore	Does not return token w/in 30 seconds	Does not eat food for 30 seconds
Share	Allows partner to take token (no protest)	Allows partner to take food (no protest)
Reject	Push out token	Push away food

Table S2. Description of dependent variables for returning the tokens and accepting the rewards.