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

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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.

Keywords: squirrel monkey; *Saimiri* spp.; inequity; exchange; convergent evolution

1. INTRODUCTION

Several species are known to respond negatively to inequitable outcomes (*Cebus apella* [1–3], *Pan troglodytes* [4,5] and *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 (IC), 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 laboratory [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 to determine whether inequity responses are due to homology or convergence related to cooperation.

2. MATERIAL AND METHODS

Twenty-four adult squirrel monkeys (*Saimiri sciureus* and *Saimiri 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 per cent 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 the electronic supplementary material.

To test whether the squirrel monkeys responded when the other received a different reward (either a HVR 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 an 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

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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 an MVR. To test the hypothesis that the inclusion of a task elicits a different response, we compared the IB with 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 signed-rank exact tests (analyses were repeated with repeated-measures ANOVAs to take into account possible nesting, despite the marginal sample size for parametric tests; see the electronic supplementary material). 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 $\kappa = 0.995$).

3. RESULTS AND DISCUSSION

Squirrel monkeys varied in their rate of refusal among the four conditions (figure 1 and see also electronic supplementary material, figure S1; Friedman's test, $n = 24$, $\chi^2 = 32.309$, d.f. = 3, $p < 0.001$). However, they did not respond differently when their partner got a better reward as compared with when both got the same, lower value outcome (comparing IB with 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 with when they were given the same lower value reward (comparing IC with 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 with IC: $T+ = 50.5$, $n = 21$, $p = 0.023$).

Previous results have found sex differences in responses [5], thus, we also analysed males and females separately. Neither males nor females refused more often in the IB than the EC condition (comparing IB with 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 with 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 with 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 versus GR: $T+ = 283$, $n = 24$, $p < 0.001$; males:

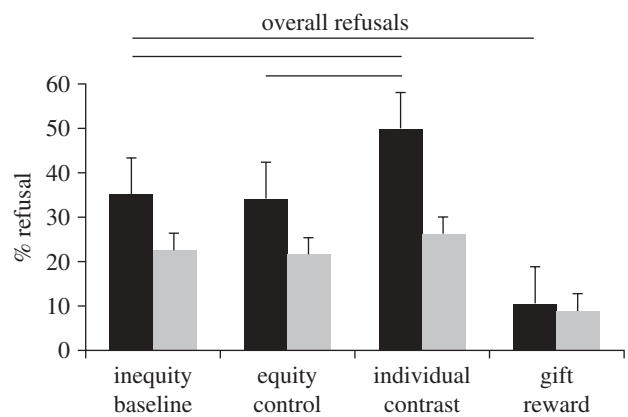


Figure 1. Mean percentage \pm s.e.m. of total refusals (token and food refusals combined) in each condition male and female subjects (see the electronic supplementary material, table S1 for details of each condition). Bars indicate significant pairwise comparisons for males. Black bars, males; grey bars, females.

$T+ = 102$, $n = 14$, $p = 0.002$; females: $T+ = 18$, $n = 6$, $p = 0.115$; see the electronic supplementary material, 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 [3,5].

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 with 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 probably correlated with cooperation among 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 behaviour's function.

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