

Inequity responses of monkeys modified by effort

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Without joint benefits, joint actions could never have evolved. Cooperative animals need to monitor closely how large a share they receive relative to their investment toward collective goals. This work documents the sensitivity to reward division in brown, or tufted, capuchin monkeys (*Cebus apella*). In addition to confirming previous results with a larger subject pool, this work rules out several alternative explanations and adds data on effort sensitivity. Thirteen adult monkeys exchanged tokens for rewards, showing negative reactions to receiving a less-favored reward than their partner. Because their negative reaction could not be attributed to the mere visibility of better rewards (greed hypothesis) nor to having received such rewards in the immediate past (frustration hypothesis), it must have been caused by seeing their partner obtain the better reward. Effort had a major effect in that by far the lowest level of performance in the entire study occurred in subjects required to expend a large effort while at the same time seeing their partner receive a better reward. It is unclear whether this effort–effect was based on comparisons with the partner, but it added significantly to the intensity of the inequity response. These effects are as expected if the inequity response evolved in the context of cooperative survival strategies.

capuchin monkey | *Cebus apella* | cooperation | frustration | fairness

The recent discovery that monkeys respond negatively to unequal reward distributions (1) has generated wide interest among primatologists as well as economists (2–6). Humans, too, respond negatively to unequal treatment, sometimes doing so even in cases in which the inequity advantages themselves (7–9).

A negative response to inequity probably evolved in a context in which parties cooperate without knowing in advance how the payoffs will be distributed. In chimpanzees (*Pan troglodytes*), reciprocity may be more important than social dominance in deciding who gets how large a share (10). For example, regardless of rank in the group, wild male chimpanzees who fail to contribute to a cooperative hunt are less successful than the hunters themselves in obtaining a share of the meat (11; but see ref. 12), which might reflect recognition of effort. Because coordinated hunting is also known of capuchin monkeys [*Cebus* spp. (13, 14)], these primates face the same problem of payoff division after collective effort.

When primates work together to secure resources, success is positively correlated with the level of tolerance during subsequent resource division (15, 16). The tendency to share thus feeds back into the tendency to cooperate. In fact, when capuchin monkeys are given a chance to cooperate for unequal rewards, only those pairs that spontaneously alternate high-value rewards between themselves prove successful (17). This behavior makes monopolization of gains by dominant individuals a short-sighted strategy: in the long run, equitable outcomes produce benefits to both the dominant and the subordinate party. If this hypothesis is indeed the evolutionary origin of negative reactions to inequity in nonhuman primates, it resembles the explanation given for the evolution of inequity aversion in our own species (18–20) [although equity may be preferred even outside the context of cooperation (21)]. Of course, inequity aversion implies that humans respond negatively to inequity that benefits them as well as inequity that costs them. Whereas the majority of studies, including the

present one, test only responses to “disadvantageous (costly) inequity,” there is a great need for testing of both kinds to determine any true sense of “fairness” (2).

Before comparisons between human and nonhuman inequity responses can be profitable, however, it needs to be verified that what other primates react to is indeed distributional inequity and not some other feature of the situation. The purpose of the present work is to elucidate this issue by teasing apart the potential variables involved. The response could depend on (i) direct comparison by the subject of its own rewards and those of its partner; (ii) individual experience with better rewards; or (iii) the mere sight of such rewards. Additional variables to be considered are the effort required to secure rewards and the nature of the social relationship between partners. In both human and nonhuman primates, the strength of the inequity response seems inversely related to relationship closeness (7, 22, 23). Sharing of rewards, sensitivity to inequity, and successful cooperation seem to be products of the tolerance engendered by a close social relationship.

In the original inequity experiment, brown capuchin monkeys performed a simple exchange task in which they returned a token to the human experimenter for a food reward (1). In some tests, subjects received a piece of cucumber, just like their partner, but in other tests, the partner first received a far superior reward, a grape, followed by the subject still receiving only a piece of cucumber. Performance on the task dropped sharply (e.g., subjects returned fewer tokens and accepted fewer rewards) if the partner received a superior reward compared with situations in which both received the same reward. These results were replicated with chimpanzees (23).

An alternative hypothesis is that the mere sight of valuable food explains the drop in performance (24, 25), hence a response caused by “greed” rather than “envy.” Accordingly, the observed negative reaction does not result so much from what the partner receives, but from the mere availability of high-quality rewards. Even though this greed hypothesis was unsupported by a control built into the original experiment (2, 24), more rigorous controls are possible and have been included in the present work.

A second alternative hypothesis, which, like the greed hypothesis, focuses on the individual and its experiences rather than the relationship with the partner, is the frustration hypothesis. Accordingly, subjects react with frustration to the contrast between food currently available and superior food received on previous occasions. Thus, the cucumber recipient may be reacting to the contrast between its food and grapes that it received in previous testing. A recent study confirmed such a contrast effect in capuchin monkeys, which rejected cucumber more after

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Abbreviations: Eq, equality; Eq-G, equality with grape visible; Ineq, inequity; NS, not significant.

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first having received grapes (4). In the latter experiment, however, the monkeys also showed negative reactions to inequity, and the authors neglected a statistical comparison between both effects. Moreover, this work did not replicate the methodology of the original study in that the monkeys were not required to perform a task (26).

Task performance may turn out to be critical because two studies, one concerning the same monkeys as in the original inequity study, failed to find negative reactions to unequal food distribution if food was simply given for “free” instead of as a reward for a task (27, 28). Food provisioning apparently exerts quite a different influence on behavior than food handed out item-by-item contingent on task performance. This difference fits the above hypothesized evolutionary background of the inequity response, which emphasizes a comparison between individual payoffs for effort, not merely individual access to food.

Simply being handed food is commonplace in captivity, and finding food is commonplace in the wild. These situations may not be sufficient to trigger the inequity response. The addition of a task probably changes the monkeys’ perception of events, creating an expectation of rewards commensurate with their own and others’ effort. The original study indicated an effect of effort above and beyond the effect of reward distribution (1), but at the time this issue was not explored in depth.

The purpose of the current work is to examine the inequity response in a way directly comparable with the original study but taking into account alternative hypotheses and further details of the inequity response for a deeper understanding of the monkeys’ behavior. We also used a larger subject pool, including both genders, while employing the same simple barter task used before because, as argued above, task performance may be key to an inequity response.

Results and Discussion

This work used a paradigm similar to that of the original Brosnan and de Waal study (1). Subjects were paired and given food rewards, either immediately after a successful exchange or, for some conditions, without exchange. Rewards were pieces of cucumber and grapes, which all subjects preferred to cucumber at least 90% of the time. Dependent measure was the “typical exchange” or exchanges completed within 5 s (for more details, see *Methods*).

This work included a condition in which food rewards were shown to the subject before completing the exchange (visible-reward exchanges) to complement the original condition in which rewards were indicated only after a successful exchange. If reward expectation (independent of what the partner received) is a factor in exchange performance, we expect more refusals when rewards are visible. However, for none of the nine conditions did the two methods of exchange yield significantly different results (Wilcoxon tests comparing individual performance). Because payoffs were the same throughout the session, to keep the subjects from responding based on expectations of changing rewards, subjects may have learned what to expect, and seeing the rewards before a specific trial may not have been as salient as in situations with greater uncertainty. For analysis, the data were averaged for the two conditions.

Replication Using the Typical Exchange Measure. To verify the presence of the previously found inequity effect (1), the three basic conditions without effort variation were first analyzed, i.e., equality (Eq), equality with grape visible (Eq-G), and inequity (Ineq). The results (Fig. 1) show a significant drop in typical exchange during the Ineq compared with the Eq conditions (Wilcoxon test Ineq vs. Eq: $n = 13$, $T = 14$, $P < 0.025$; Ineq vs. Eq-G: $n = 13$, $T = 18$, $P < 0.05$, both one-tailed) but no difference between the two Eq conditions, hence no indication

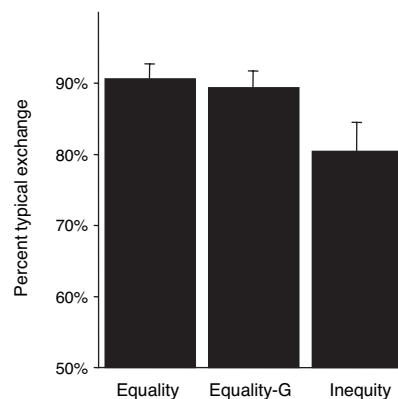


Fig. 1. Percentage of typical exchanges in three conditions with the same level of effort. Typical exchanges were those in which subjects completed the interaction in 5 s and accepted the reward. Equality test, both receive cucumber; Equality-G, Equality test with grapes visible; Inequity test, partner receives grape, subject receives cucumber.

that the visibility of grapes matters [Wilcoxon Eq vs. Eq-G: $n = 10$ [†], $T = 22.5$, not significant (NS)]. The latter lack of effect argues against the greed hypothesis, according to which Eq-G should give results closer to the Ineq than the Eq test because of the visibility of the better food reward.[‡]

No significant differences were found between male and female subjects in their performance on the three basic test conditions (Mann–Whitney U test for $N_1 = 9$ females, $N_2 = 4$ males: Eq, $U = 15.5$, NS; Eq-G, $U = 10.5$, NS; Ineq, $U = 16$, NS), nor was there a sex difference in the effect of inequity (measured as the difference in typical exchange between Eq and Ineq conditions; $U = 18$, NS).

Performance Over Time. In the original study, subjects increased their rate of refusal as sessions progressed in conditions in which a higher valued reward was given to a partner, but not if a higher valued reward was merely visible (1, 2, 24). Replicating this analysis, again by using the number of refusals to exchange, for the three main conditions without effort variation, i.e., Eq, Eq-G, and Ineq, we found the same difference in slope [Zar’s method for comparing the slopes of regression lines (29), $P < 0.05$]. As can be seen in Fig. 2, the effect of inequality is limited to the second half of the test session, indicating that it is a relatively delayed response. This analysis provides further evidence against the greed hypothesis because the changes in behavior are not based on seeing the higher-value reward but rather on seeing a partner receive it.

Frustration Effect. There has been debate about whether individuals respond negatively to receiving cucumber after previously having experienced favored foods (4, 26) because of the frustration effect (30). However, a previous study claiming primacy of the frustration effect (4) had serious methodological flaws (26). In the current work, conditions were randomized, and individuals served as both subjects and partners, so no subject

[†] N varies because ties are excluded from Wilcoxon tests.

[‡]The typical exchange measure employed in the present work differs from the measure used in ref. 1, which concerned refusals to exchange or to consume rewards. Using the latter measure, subjects showed fewer refusals in the Eq than the Ineq test (Wilcoxon Eq vs. Ineq: $n = 9$, $T = 6$, $P < 0.05$, one-tailed). The Eq-G test showed an intermediate outcome, not significantly different from either the Eq or Ineq test (Wilcoxon Eq vs. Eq-G: $n = 9$, $T = 11$, NS; Ineq vs. Eq-G: $n = 11$, $T = 26$, NS, both one-tailed). This result may mean that greed, or the desire for a better reward, plays a somewhat stronger role in whether subjects complete the interaction at all rather than in a typical fashion, although these results also suggest that inequity is a stronger factor than greed.

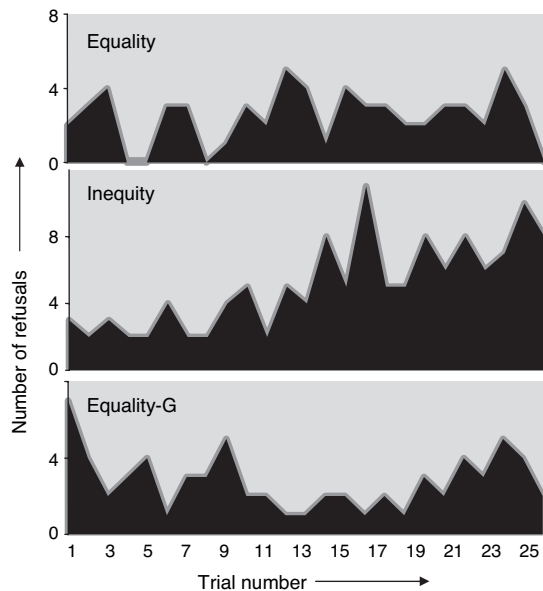


Fig. 2. In the Ineq sessions, in which their partners received a better reward, subjects increased their likelihood of refusing to exchange over the course of the 25 trials. In Eq and Eq-G sessions, the subject's willingness to exchange did not change over the course of the session.

completed more than four sessions before having received a grape in at least one session. Thus, we could test the frustration effect by comparing test performance based on food received in the immediately preceding test, regardless of whether the individual acted as a subject or partner. Given the claim that the frustration effect can explain all results (4), we combined the three main conditions in which the subject received cucumber (i.e., Eq, Eq-G, and Ineq).

The most rigorous evaluation on the effect of past testing is to compare responses across four possible preceding reward distributions. How did the subject respond dependent on whether previously (i) both individuals had received cucumber; (ii) the subject had received cucumber but its partner a grape; (iii) the subject had received a grape but its partner cucumber; and (iv) both individuals had received grape. We did not have all of these conditions for all subjects, but we were able to test typical exchange with a Friedman's test and found no indication that responses varied (Friedman's $\chi^2 = 0.868$, $df = 3$, $P = 0.833$). We then collapsed the above four conditions into two: tests conducted after the subject had received either (i) a grape or (ii) a cucumber in the previous test. We found very similar results. Typical exchange after a test that rewarded a grape (mean \pm SEM, "frustration": $85.4 \pm 3.4\%$) was very similar to that after a test which rewarded a cucumber ("no-frustration": $87.6\% \pm 2.1\%$). Significant differences existed neither for the overall results (Fig. 3; Wilcoxon: $n = 13$, $T = 36$, NS) nor if tested for each of the three conditions (Eq, Eq-G, or Ineq) separately. The frustration effect predicts reduced performance by subjects receiving cucumber after sessions in which they had received a grape. Yet, no change in performance was detectable, thus ruling out the frustration effect as an explanation.

Effect of Effort and Reward. The importance of effort, hinted at before (1), was clearly evident in the present work. Because the "large-effort" conditions contained multiple exchanges per session (and hence are not exactly comparable with the "small-effort" conditions), for the purpose of this analysis the frequency of typical exchanges is calculated as trials in which subjects completed each exchange within 5 s and consumed the reward.

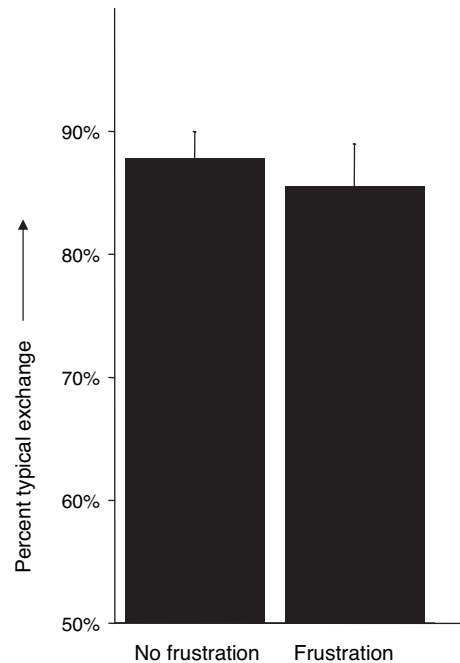


Fig. 3. There was no evidence of a frustration effect. Subjects showed typical exchanges at about the same rate in sessions immediately after those in which they had received grapes (frustration) as in those after sessions in which they had received only cucumber (no frustration).

We first compared the four effort conditions in which subjects received cucumber. To do so, we normalized the data by ranking for each subject its typical-exchange performance across these conditions (Eq-Ef1, Eq-Ef3, Ineq-Ef1, and Ineq-Ef3). These ranked data were then subjected to a repeated-measures ANOVA with two reward conditions (Eq or Ineq) and two effort conditions (the subject exchanges either once or three times). The result was a significant effect of both effort ($F_{1,12} = 15.32$, $P = 0.002$; see Fig. 4) and reward distribution ($F_{1,12} = 16.67$, $P = 0.002$), as well as a significant interaction between the two ($F_{1,12} = 16.76$, $P = 0.001$).

Pairwise comparisons of the four conditions show no significant effect of reward distribution for the large-effort difference (Wilcoxon test: Eq-Ef3 vs. Ineq-Ef3, $n = 12$, $T = 18.5$, NS), indicating that subjects do not distinguish reward differences when the required effort is great. However, there exists a significant effect of reward distribution for the small-effort difference (Eq-Ef1 vs. Ineq-Ef1, $n = 13$, $T = 2$, $P < 0.005$, one-tailed), again confirming an inequity response in these monkeys.

If reward condition is held constant, variation in effort yields significant results. When both individuals receive the same reward, subjects exchange significantly less when their effort required is greater (Eq-Ef1 vs. Eq-Ef3, $n = 12$, $T = 2$, $P < 0.005$, one-tailed). When the subject is doubly disadvantaged by both receiving a lesser reward and putting in more effort, there remains a significant difference in the predicted direction between large and small effort, with subjects responding more slowly in the greater-effort condition (Ineq-Ef1 vs. Ineq-Ef3, $n = 11$, $T = 11$, $P < 0.05$, one-tailed).

It is unclear from the above analysis whether the effect of effort is the result of the subject's own effort, which can be great or small, or the difference in effort with the partner for any given trial, who, under these conditions, never performs a task. There is one direct-effort comparison possible, however, between the basic Eq condition (subject exchanges once, partner exchanges

rated. Dependent offspring were always allowed into the test chamber with their mothers. All subjects had extensive experience with the test chamber and separation procedures. Monkeys acted as both subjects and partners throughout the study. Whenever possible, an individual did not serve as the subject in two consecutive tests. No monkey ever participated in more than one testing session per day (regardless of their role as subject or partner).

Task. The monkeys received food for performance of a simple exchange task (35–37). Exchange consisted of the experimenter placing the token (a small granite rock) into the test chamber, then standing in front of the test chamber with right hand outstretched, palm up, as a begging gesture. Subjects received a reward upon the placement of the token into the experimenter's hand. Tokens that were thrown out of the test chamber or were not placed into the experimenter's hand were not rewarded.

To determine how expectations affected the monkeys' behavior, two methods to exchange the token for a reward were used. In the visible-reward condition, food was held up in the experimenter's left hand from the time the token was given until the subject completed the exchange, at which point they received the reward. In the hidden-reward condition, no reward was held up until after the token had been returned by the subject [this method was the same as in the original study (1)]. Rewards were present in clear bowls during all sessions. In both conditions, unless otherwise stated, both rewards were visible to both the subject and the partner at all times.

Before testing, all subjects participated in a series of food preference tests to verify their preference for a single grape (the high-value food) over one-quarter of a slice of cucumber (the low-value food). The subject had to make a choice between two simultaneously offered food items, of which it could obtain only one, held out by the experimenter in different hands separated by ≈ 10 cm. Ten choices were offered with reward position alternating between left and right (35).

Test Conditions. Subjects participated in nine testing conditions, which all consisted of two individuals sitting side-by-side in the two sections of the test chamber (Fig. 5). Each condition was run twice, once using the visible-reward condition and one using the hidden-reward condition. Subjects completed one condition before beginning the next. Subject's initial condition was determined randomly, but half of the males and half of the females began with each condition.

Each test session consisted of 25 trials of a single variation. The order of sessions for each subject was randomized before the commencement of testing. For each trial, the partner exchanged first, followed by the subject.

Reward variation. Eq test. Both partner and subject exchanged for cucumber. No grapes were visible at any point (*cf.* ET in ref. 1).

Eq-G test. This test was the same as Eq, but before every trial the experimenter waved the clear bowl with grapes in front of the monkeys. Grapes remained visible throughout the session. This condition, similar to one in ref. 23, replaced the food-control condition (1), in which subjects were tested alone.

Ineq test. The partner exchanged for a grape, after which the subject exchanged for cucumber (*cf.* IT in ref. 1).

Effort and reward variation. As described below, both efforts and rewards were varied. In conditions that involved multiple exchanges, each exchange was performed separately, and subjects had 60 s for each of the three exchanges. However, the trial was terminated at the first refusal or failure to exchange.

Both cucumber–more effort (Eq-Ef1). The partner received cucumber for free (i.e., without exchange), after which the subject exchanged once for cucumber (effort difference = one exchange). No grapes were visible.



Fig. 5. A monkey in the test chamber returns a token to the experimenter with her right hand while steadying the human hand with her left hand. Her partner looks on. This is a hidden-reward exchange, i.e., the monkey does not see the reward she is to receive before successful exchange. (Drawing by Gwen Bragg and Frans de Waal after a video still.)

Both cucumber–much more effort (Eq-Ef3). This test was the same as Eq-Ef1, except that the subject must exchange three times for cucumber (effort difference = three exchanges).

Both grape–more effort and both grape–much more effort. The above Eq-Ef1 and Eq-Ef3 conditions were repeated using grapes for both individuals instead of cucumber, which was not visible during the test.

Less reward–more effort (Ineq-Ef1). The partner received a grape for free, after which the subject exchanged once for cucumber (*cf.* EC in ref. 1).

Less reward–much more effort (Ineq-Ef3). This test was the same as Ineq-Ef1 except that the subject exchanged three times for cucumber.

Exchange Measure. The percentage of successful exchanges, reward refusals, and failures to exchange was recorded for each test. A successful exchange was defined as one in which the subject returned the token and ate the offered reward. Reward refusals occurred when the subject returned the token but failed to eat the reward within 15 s of it being offered (occasionally subjects would consume ignored rewards at a later point; however, such actions were still coded as a refusal because they deviated from typical exchange). A failure to exchange occurred when the subject either failed to return the token within the 60 s allotted (latency to exchange was considered the time from the placing of the token in the test chamber to the subject's returning

