

uncertainty into the future, and this is carried through in the transformed series. Other historical SST series could be substituted; the changes to the pattern are minor to negligible (Supplementary Information).

Computing probabilities of recurrence

Subsets of data were extracted for warmest months, three warmest months and averaged warmest quarters of each year. Residuals of all but one (Alphonse atoll) warmest month series have normal distributions (Kolmogorov–Smirnov tests). Warmest quarters' residuals are also normally distributed in all sites except one (granitic Seychelles). As time proceeds, the difference between the lethal 1998 SST value (also expressed as a residual) and the normally distributed population of SSTs decreases. For each month, '1 – normdist' determines the probability that each site's lethal temperature is part of the site's population of temperatures. This yields probability curves of repeat recurrences of the peak temperature of 1998.

In the warmest 3-month data sets, residuals in only half of the sites have normal distributions (they lack extended 'tails'). For these, 'bootstrap tests' were used instead of the normdist function to compute probability; probability was the number of residuals in the whole data set with a value greater than the test value, divided by the total number. Curves almost exactly match those obtained by the normdist method. This test was also used for the north Seychelles site for the quarterly series to extend that transect northwards; the test differed by less than 1 year from that obtained with the normdist function at that site.

'Lethal' SSTs and timing

Peak SSTs ranged from February in the south to September in the northwest. For 27 sites, the warmest quarter was the peak month with the preceding and the following months. For the other six sites, it was the peak month with the two preceding months. For the warmest month and 3-month tests, the test SST value was the warmest 1998 HadISST1 temperature. For the warmest quarter test, the average SST of the warmest 3 months was used. These temperatures were generally only less than 0.2 °C warmer than any earlier recorded temperatures at that site.

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Monkeys reject unequal pay

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During the evolution of cooperation it may have become critical for individuals to compare their own efforts and pay-offs with those of others. Negative reactions may occur when expectations are violated. One theory proposes that aversion to inequity can explain human cooperation within the bounds of the rational choice model¹, and may in fact be more inclusive than previous explanations^{2–8}. Although there exists substantial cultural variation in its particulars, this 'sense of fairness' is probably a human universal^{9,10} that has been shown to prevail in a wide variety of circumstances^{11–13}. However, we are not the only cooperative animals¹⁴, hence inequity aversion may not be uniquely human. Many highly cooperative nonhuman species seem guided by a set of expectations about the outcome of cooperation and the division of resources^{15,16}. Here we demonstrate that a nonhuman primate, the brown capuchin monkey (*Cebus apella*), responds negatively to unequal reward distribution in exchanges with a human experimenter. Monkeys refused to participate if they witnessed a conspecific obtain a more attractive reward for equal effort, an effect amplified if the partner received such a reward without any effort at all. These reactions support an early evolutionary origin of inequity aversion.

In preliminary studies, two conditions were used: 'equality', in which two monkeys exchanged tokens with a human experimenter

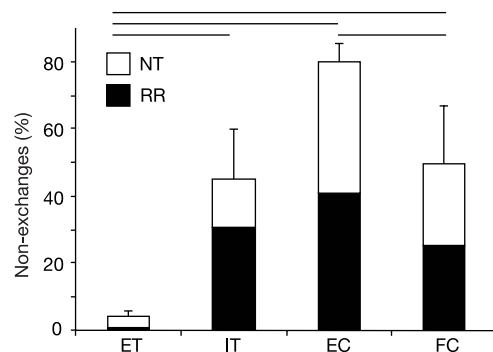


Figure 1 Mean percentage $\pm$ s.e.m. of failures to exchange for females across the four test types. Black bars (RR) represent the proportion of non-exchanges due to refusals to accept the reward; white bars (NT) represent those due to refusals to return the token. s.e.m. is for combined non-exchanges. Lines indicate significant differences between conditions (Tukey's multiple comparisons). ET, equality test; IT, inequality test; EC, effort control; FC, food control.

to receive cucumber, and 'inequality', in which one monkey exchanged for cucumber and its partner for grape, a more favoured food. Whereas in previous tests males and females had been equally reliable exchangers, only females reacted differently to the two conditions. Compared with equality tests, females receiving the less favoured reward in inequality tests were less willing to exchange, whereas males showed no such effect. Our limited sample size did not allow a conclusive comparison of the sexes, but independent evidence indicates that capuchin females pay closer attention than males to the value of exchanged goods and services^{17,18}.

The study reported here concerns only five females, which were again subjected to the equality and inequality conditions plus two new controls: 'effort controls', in which a grape was simply handed to the partner by the experimenter (no exchange) followed by the subject herself exchanging for cucumber, and 'food controls' in which, in the absence of a partner, the subject witnessed a grape being placed in the location where the partner normally sat, after which the subject herself exchanged for cucumber. For this test, grapes accumulated every trial, as it would have been too disruptive to remove them. We measured the monkeys' rate of and latency to successful exchange. Although available rewards were visible to both monkeys, neither was shown which reward they would receive before successfully returning the token. We divided incomplete exchanges into two categories: (1) failure to hand back the token (no token, NT), and (2) failure to accept or eat the proffered reward (reject reward, RR). Both kinds of incomplete exchanges often involved active rejection, such as tossing the token or reward out of the test chamber.

Despite the small number of subjects, the overall exchange tendency varied significantly across the four conditions in a manner indicating that the presence of high-value rewards reduced the tendency to exchange for low-value rewards ($F_{3,16} = 25.78$, $P < 0.001$; Fig. 1). This effect was enhanced by a difference in effort between partners (Tukey's multiple comparisons comparing effort controls with food controls, $P < 0.05$; and effort controls with equality tests, $P < 0.05$). Thus, the strongest increase in refusal to exchange occurred if a partner received better rewards without any effort.

Exchange behaviour may change over the course of a test. Each subject received two tests of each condition, each with 25 trials (exchanges). Failed exchanges (NT plus RR, see above) might increase over consecutive trials if subjects did not immediately recognize that they were receiving a lesser reward, but learned over time. Conversely, failed exchanges might decrease if subjects gradually 'settled' for the lesser reward, seeing that no higher-value reward was forthcoming. We tested these contrasting predictions by comparing each subject's responses during the first 15 versus the last 10 trials per tests. We ran the required exact Wilcoxon signed ranks

test, which given our sample size could not reach a P -value below 0.06. For equality, inequality and effort control conditions, non-exchanges increased over the course of tests, reaching the minimum P -value only for the effort controls (equality: $T = 9$, $n = 4$, $P = 0.25$; inequality: $T = 13$, $n = 5$, $P = 0.18$; effort control $T = 15$, $n = 5$, $P = 0.06$; Fig. 2). For the food controls, in contrast, non-exchanges decreased over the course of tests ($T = -15$, $n = 5$, $P = 0.06$). This last condition differed from the others in that no other individual was present. Perhaps this made adjustments to low-value rewards easier.

Failure to exchange was roughly equally divided between no token exchange (NT, 45.4%) and no food acceptance (RR, 54.6%). Each measure separately showed significant variation across the four conditions (NT, $F_{3,16} = 8.43$, $P = 0.001$; RR, $F_{3,16} = 7.73$, $P = 0.002$; Fig. 1), mainly due to a significant difference in exchange between the equality test and the other three conditions. The general tendencies across the four conditions were the same for NT and RR (Fig. 1), indicating that conditions affected these responses similarly.

Failure to hand back a received token (NT) is a highly unusual response in our trained capuchins: in two years of bartering, such failures occurred in less than 5% of trials, as also seen in the equality test. The marked increase in failure to exchange in individuals receiving the lower-value reward in the inequality test and the two control conditions cannot be explained by the absence of positive reinforcement, as rewards continued to be cucumber, an accepted reward in the equality test. Even more curious than a drop in the conditioned response rate was the second manner in which exchanges failed: refusal to accept or consume the reward (RR). In doing so, subjects forfeited a directly accessible food that they readily accept and consume under almost any other set of circumstances. One possible explanation is that reward rejections relate to violated expectations, in which monkeys forego a low-value reward if a high-value one is anticipated¹⁹. On the basis of her own reward history, however, there would seem no reason for a subject receiving cucumber to expect anything else during the same test. If expect-

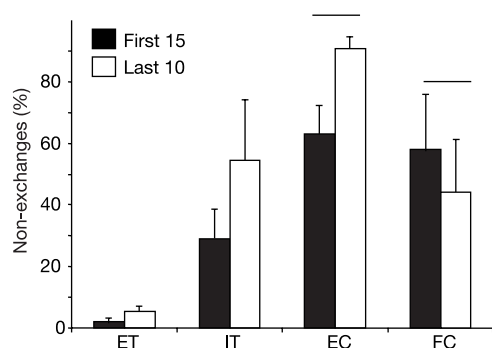


Figure 2 Mean percentage $\pm$ s.e.m. of failures to exchange in the first 15 trials (black bars) versus the last 10 trials per test (white bars). Lines indicate differences at $P = 0.06$ (exact Wilcoxon signed ranks test). ET, equality test; IT, inequality test; EC, effort control; FC, food control.

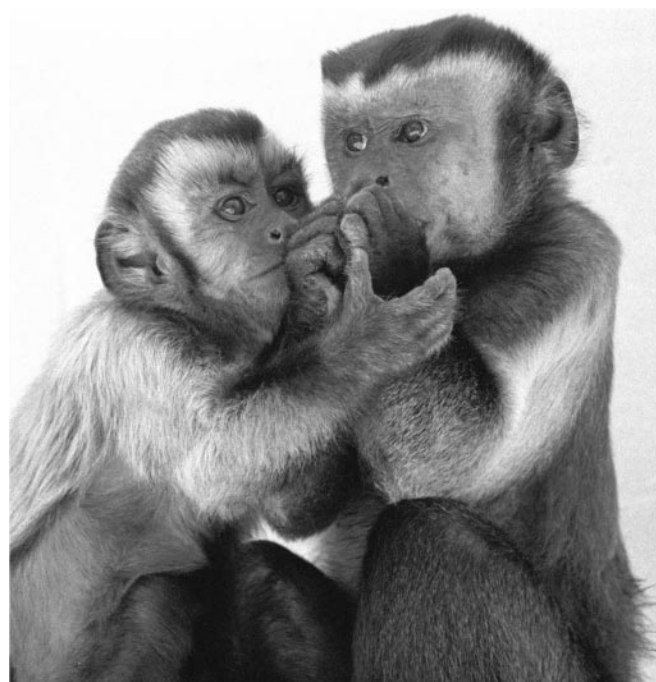


Figure 3 A juvenile capuchin monkey shows cheek-to-cheek begging to an eating adult male, cupping his hand next to the adult's food in solicitation. This primate is exceptionally tolerant and readily shares food, which may be a precondition for the reported reactions to reward division.

tations do have a role, therefore, they must be based on the visible presence of inaccessible high-value rewards. The general increase in refusals to exchange in the course of testing supports this argument. Food controls, in which a partner was absent, differed by showing a decrease in refusals. This suggests that expectations are based on seeing a partner receive and/or eat high-value rewards rather than the mere presence of such rewards.

Finally, when measuring the latency to exchange for all successfully completed exchanges (that is not including NT non-exchanges), we found significant variation across the four conditions ($F_{3,16} = 321.33$, $P < 0.001$), and significant variation between all conditions (Tukey's multiple comparisons). The capuchins completed exchanges most quickly in inequality tests, and more slowly in the control tests than in equality tests. This result is hard to interpret, but precludes the possibility that the mere presence of grapes either excited subjects into more rapid exchange or diverted their attention, thus slowing exchange. Grapes were visible under all conditions except equality tests.

People judge fairness based both on the distribution of gains and on the possible alternatives to a given outcome^{20,21}. Capuchin monkeys, too, seem to measure reward in relative terms, comparing their own rewards with those available, and their own efforts with those of others. They respond negatively to previously acceptable rewards if a partner gets a better deal. Although our data cannot elucidate the precise motivations underlying these responses, one possibility is that monkeys, similarly to humans, are guided by social emotions. These emotions, known as 'passions' by economists, guide human reactions to the efforts, gains, losses and attitudes of others^{22–25}. Clearly if these reactions evolved to promote long-term human cooperation²⁶, they may exist in other animals as well²⁷. It has been proposed that nonhuman primates are guided by species-typical expectations "about the way in which oneself (or others) should be treated and how resources should be divided"¹⁵. As opposed to primates marked by despotic hierarchies, tolerant species with well-developed food sharing and cooperation, such as capuchins (Fig. 3)^{16,18,28–30}, may hold emotionally charged expectations about reward distribution and social exchange that lead them to dislike inequality. □

Methods

Five adult female and five male (three adult and two subadult) capuchin monkeys from two long-term, stable social groups were initially tested, although only the females completed all testing. Experiments were carried out in a familiar test chamber, which was divided by a mesh partition into two equally sized (36 × 60 × 60 cm) compartments. For testing, the subject and partner were enclosed in these adjoining compartments and had visual, vocal and limited tactile contact (that is, both monkeys of an experimental pair were close enough to clearly observe the exchanges and rewards of the other). To minimize distractions from their group, an opaque panel backed the test chamber, allowing some vocal but no visual or tactile contact. For details about the testing facility, see ref. 18.

For exchange, the subject was given a token that could immediately be returned to the experimenter for a food reward. The experimenter (S.F.B.) stood before the monkey with the left hand outstretched in a palm-up begging gesture, approximately 5 cm above the floor of the test chamber and 2 cm from the mesh, and with the right hand in the laboratory coat pocket. No other cues were given to encourage the monkey, and no reward was shown before correct exchange. The monkey had 60 s to place the token into the palm of the experimenter's outstretched hand. Throwing the token at the experimenter or out of the test chamber did not count as an exchange. After a successful return, the experimenter lifted the correct reward from a transparent bowl visible to both monkeys and gave it to the exchanger. In cases of failure to exchange, no reward was shown. Exchange interactions were typically completed in about 5 s, and all subjects exchanged successfully in 95% or more of the baseline tests. All subjects had at least 2 yr experience with the exchange scheme, but none had been used previously in any similar study.

Tokens were small granite rocks (2–3 cm in diameter). The lower-value food item was one-quarter of a cucumber slice and the higher-value food item was a grape. In dichotomous choice tests, grapes were preferred at least 90% of the time to cucumber by all capuchins, but all capuchins readily exchanged for cucumber in the absence of other rewards (for example, equality test). Food preferences did not change throughout the testing period.

Capuchins were paired with a same-sex partner who remained the same throughout the study. The exception was the food control test, in which subjects were tested alone. Monkeys were never used in more than one test per day. Each condition was tested twice, on different days, with each test consisting of 50 alternating trials (25 per

individual) beginning with the partner. Each monkey had 60 s to exchange, and after either 60 s or the completion of an exchange, whichever came first, the other monkey's exchange commenced. No break, other than that necessary for the exchanger to prepare (5–10 s), was added between trials, to assure that subjects remembered the previous exchange. The presence of a partner consuming a reward did not visibly affect the subjects' behaviour during exchange. All tests consisted of trials of one condition only. Each capuchin was tested on all four conditions: equality, inequality, effort control and food control.

Failures to exchange were divided into refusals to return the token and refusals to accept the reward. Data were collected during testing by a second experimenter, who remained the same throughout the study, with supplementary data obtained from videotapes. All experiments were videotaped using a Canon GL-1 digital camcorder, time stamped to 100th of a second. Friedman's tests were used to compare individuals' mean failure to exchange across test types, and pair-wise comparisons were conducted using Tukey's multiple comparisons. When comparing exchange rate in the first and second half of tests, exact Wilcoxon signed ranks tests were used. All reported P -values are two-tailed.

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