

Animal behaviour

Fair refusal by capuchin monkeys

Brosnan and de Waal¹ report that capuchin monkeys show evidence of a sense of fairness or 'inequity aversion' because they rejected a less preferred reward when they saw a partner monkey receive a preferred reward for the same task. However, this does not show that monkeys are averse to inequity, only that they reject a lesser reward when better rewards are available. There are risks inherent in seeking anthropomorphic explanations for non-human behaviour.

In the 'inequality test', the monkeys refused to exchange a token for a cucumber slice (non-preferred reward) on 43% of trials when they saw a partner monkey receive a preferred grape reward for the same effort. However, in the 'food control' condition, in which the partner was not present, these same monkeys were just as likely to refuse the cucumber slice when they saw a grape placed where the partner normally sat (49% refusals). There can be nothing inequitable about receiving a non-preferred reward if nobody is receiving anything better. In the food-control condition, the monkeys are refusing the non-preferred reward simply because they can see that a better reward is potentially available. This is therefore the most parsimonious explanation for their refusal to accept the non-preferred reward when they see another monkey receive a better one.

Brosnan and de Waal¹ reject this reward-availability explanation for two reasons. First, in a third condition (the 'effort control' condition), where monkeys saw their partner receive a grape without having to exchange a token, the monkeys were more likely to refuse the cucumber slice than in the food-control condition. On its own, the comparison of the effort-control and food-control conditions is in the direction required by a fairness account. But fairness cannot account for the equally large difference between the effort-control and inequality-test conditions.

The basis of Brosnan and de Waal's second reason for rejecting the reward-availability explanation is in their Fig. 2, which seems to show an increasing trend of non-exchange for the two conditions in which another monkey was present (inequality test and effort control) and a decreasing trend of rejections in the food-control condition where no other monkey was present. Their Fig. 2 shows mean rejections for the first 10 and last 15 trials (not, as stated in the paper, the first 15 and last 10 trials; Brosnan and de Waal, personal communication) averaged across two sessions.

When the cumulative rate of rejections is

represented across all trials of both sessions for Brosnan and de Waal's monkeys, we find that there is no overall increase in rejection rate in the inequality-test and effort-control conditions, and that the rate does not decline across sessions in the food-control condition (results not shown).

Although explanations of animal behaviour in anthropomorphic terms are notoriously prone to imprecision², if 'fairness' or 'inequity aversion' mean anything in this context, they surely imply that individuals reject rewards more often when they see another receive a better reward than when the better reward is simply in view with no one else there to consume it. The very similar levels and patterns of cucumber rejection in the inequality-test and food-control conditions therefore contradict an account based on fairness or inequality.

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1. Brosnan, S. F. & de Waal, F. B. M. *Nature* **425**, 297–299 (2003).
2. Wynne, C. D. L. *Do Animals Think?* (Princeton Univ. Press, in the press).

Brosnan and de Waal reply — We have shown¹ that animals compare their own rewards with those of others, and accept or reject rewards according to their relative value. Our aim was not to demonstrate that capuchin monkeys make a human response to inequality, but rather to elucidate evolutionary precursors to inequity aversion. We use this term as in ref. 2 — "people resist inequitable outcomes; that is, they are willing to give up some material pay-off to move in the direction of more equitable outcomes" — and specifically focus on "disadvantageous inequity aversion"². The monkeys in our experiment could not change the reward division, and hence could not actively avoid inequality, but we wanted to determine whether they would at least recognize inequality if subjected to it. We found that the capuchins reacted negatively, refusing to complete the interaction.

It is unlikely that inequity aversion appeared *de novo* in humans. It almost certainly evolved because individuals who responded to inequality disadvantageous to themselves increased their relative fitness compared with those who did not. We recognize several potential evolutionary precursors to disadvantageous inequity aversion (S. F. B., H. C. Schiff and F. B. M. de W., manuscript in preparation). First is the ability to recognize that rewards and efforts differ between individuals, which is also required for social learning, a skill present in capuchins³. Second is the propensity to react if another individual receives a better reward for a specific task. Third is sacrifice to alter another individual's outcome.

Our study mainly concerned the second ability, showing that capuchin monkeys react negatively when another individual gets a better reward for the same or less effort on a specific task. This finding suggests that precursors to inequity aversion are present in animals from which our lineage split millions of years ago. Although capuchins may be reacting somewhat differently from adult humans, we have still learned something about the behaviour's possible evolutionary trajectory.

Regarding the cross-cultural study, the lowest mean offer by a proposer in the ultimatum game was 26% of the total, whereas the lowest modal offer was 15%, both by the Machiguenga of Peru⁴. Such relatively high offers would not seem to be consistent with completely selfish individuals who lack any conception of fairness⁵.

As stated earlier¹, although the mere presence of a higher-value reward affects the capuchins, their reaction is not the same as when a conspecific receives the higher-value reward. To ignore the differences between the inequality test and the food-control test is unwarranted. Our Fig. 1 does not permit any conclusions about the effect of the food-control test and was not used for this purpose; it is the data in our Fig. 2 that inspired our claim.

The frequency of refusals across trials increases when a partner receives the reward and decreases when a reward is merely visible. The conservative statistic we chose did not allow significance ($P < 0.05$)¹, but we have since subjected these data to a comparison of the slopes of the linear regressions across trials for each test⁶. This re-analysis shows that refusals in the food-control test decrease across time, whereas those in the inequality test and effort-control condition increase ($F_{2,69} = 28.71, P < 0.001$). Our subjects therefore discriminate between a situation in which higher-value food is being consumed by a conspecific and one in which such food is merely visible, intensifying their rejections under only the former condition.

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Corrigendum

When the American sea sturgeon swam east

Arne Ludwig, Lutz Debus, Dietmar Lieckfeldt, Isaac Wirgin, Norbert Benecke, Ingo Jenneckens, Patrick Williot, John R. Waldman, Christian Pitra
Nature **419**, 447–448 (2002).

The institutional address of A. L. should have been listed as the Institute of Freshwater Ecology and Inland Fisheries and Institute for Zoo and Wildlife Research.