Chimpanzees Are Rational Maximizers in an Ultimatum Game

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Traditional models of economic decision-making assume that people are self-interested rational maximizers. Empirical research has demonstrated, however, that people will take into account the interests of others and are sensitive to norms of cooperation and fairness. In one of the most robust tests of this finding, the ultimatum game, individuals will reject a proposed division of a monetary windfall, at a cost to themselves, if they perceive it as unfair. Here we show that in an ultimatum game, humans' closest living relatives, chimpanzees (*Pan troglodytes*), are rational maximizers and are not sensitive to fairness. These results support the hypothesis that other-regarding preferences and aversion to inequitable outcomes, which play key roles in human social organization, distinguish us from our closest living relatives.

Humans are able to live in very large groups and to cooperate with unrelated individuals whom they expect never to encounter again, conditions that make the standard mechanisms for cooperation unlikely (*1*), namely kin selection (*2*) and reciprocal altruism (*3*). Nevertheless, people help others, sometimes at great personal cost. But people are not obligate altruists; they do not tolerate abuse of their generosity. Not only will they punish or shun individuals who free-ride or exploit them, they will do so even if they themselves do not benefit from correcting the behavior of norm violators (*4*). The willingness both to cooperate and to punish noncooperators has been termed strong reciprocity (*5*) and has been claimed to be uniquely human (*6*). To cooperate in these ways, humans must be more than self-regarding rational decision-makers; they must also, at least to

some degree, have concern for outcomes and behaviors affecting others (other-regarding preferences) (*4*) as well as a general concern for norms of fairness (*7*, *8*).

The benchmark test for examining sensitivity to fairness and other-regarding preferences is the ultimatum game (*9*). In the standard version of the game, two anonymous individuals are assigned the roles of proposer and responder. The proposer is offered a sum of money and can decide whether to divide this windfall with the responder. The crucial feature of the ultimatum game is that the responder can accept or reject the proposer's offer. If the responder accepts it, both players receive the proposed division; if the responder rejects it, both get nothing. The canonical economic model of pure self-interest predicts that the proposer will offer the smallest share possible and that the responder will accept any nonzero offer. This is not what happens. Although the specifics vary across culture and setting, the basic finding is that proposers typically make offers of 40 to 50% and responders routinely reject offers under 20% (*10*). These findings suggest that responders are

sensitive to unfairness and punish proposers who make inequitable offers by rejecting those offers at a cost to themselves, and knowing this, proposers make strategic offers that are less likely to be refused.

The ultimatum game has been used in dozens, possibly hundreds of studies, including various human cultures (*11*) and children (*12*). Testing the ultimatum game on other species would be an important contribution to the debate on the evolution and possible uniqueness of human cooperation (*6*). Chimpanzees are our closest extant relatives and engage in cooperative behavior such as group hunting, coalitionary aggression, and territorial patrols (*13*). Furthermore, in experiments they have been shown to coordinate their behavior (*14*) and to provide help (*15*, *16*). However, there is ongoing debate about whether chimpanzees are sensitive to, and tolerant of, unfairness (*17*) or whether they simply attend to their own expectations with no regard for what others receive (*18*). Additionally, experiments have failed to reveal other-regarding preferences when food was involved (*19*, *20*) other than to punish direct theft (*21*). Having chimpanzees play the ultimatum game would address these conflicting findings on fairness and negative reciprocity and allow direct comparisons to humans.

In the current study, we tested chimpanzees in a mini-ultimatum game. The mini-ultimatum game is a reduced form of the ultimatum game in which proposers are given a choice between making one of two pre-set offers which the responder can then accept or reject (*22*). In one such study (*23*), there were four different games. In all games, the proposer had as one option an amount that would typically be rejected by a human responder as unfair, namely 80% for the proposer and 20% for the responder (8/2 offer; the proposer received the amount to the left of the slash and the responder received the amount to the right). In the 5/5 (fair) game, the proposer

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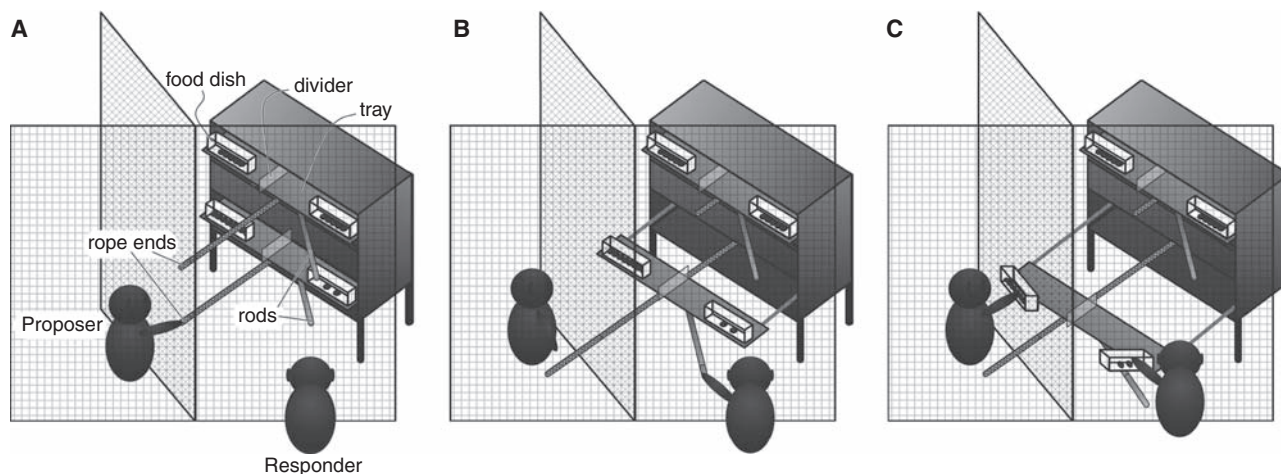*To whom correspondence should be addressed. E-mail: jensen@eva.mpg.de

Fig. 1. Illustration of the testing environment. The proposer, who makes the first choice, sits to the responder's left. The apparatus, which has two sliding trays connected by a single rope, is outside of the cages. (**A**) By first sliding a Plexiglas panel (not shown) to access one rope end and by then pulling it, the proposer draws one of the baited trays halfway toward the two subjects. (**B**) The responder can then pull the attached rod, now within reach, to bring the proposed food tray to the cage mesh so that (**C**) both subjects can eat from their respective food dishes (clearly separated by a translucent divider).

was faced with the choice of 8/2 versus 5/5. The other games were 8/2 versus 2/8 (unfair versus hyperfair), 8/2 versus 8/2 (no choice), and 8/2 versus 10/0 (unfair versus hyperunfair). Human responders rejected the 8/2 offer most when the alternative was fair (5/5 game), less when the alternative was hyperfair (2/8 game), even less when there was no alternative (8/2 game), and hardly at all when the alternative was for the proposer to be even more selfish (10/0 game) (23). The differential rejection of unfair outcomes across the games suggests that people are not sensitive solely to unfair distributions (7) nor solely to unfair intent (24) but to a combination of both (8). If chimpanzees are sensitive to unfairness and are negatively reciprocal, they would behave like *Homo reciprocans* (25), whereas if they accept any nonzero offer regardless of alternatives for the proposer, they will be more like the hypothetical *Homo economicus* (26).

Subjects were 11 chimpanzees from a group-housed colony at the Wolfgang Köhler Primate Research Center (27). The proposer sat to the left of the 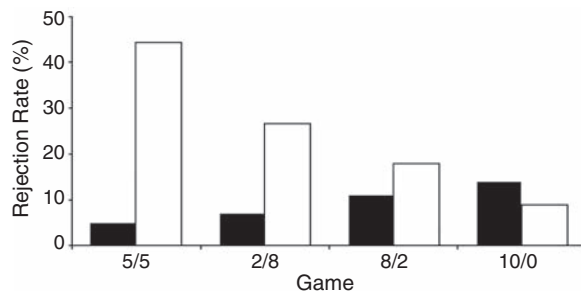responder, who was in an adjacent cage in an L-shaped arrangement. The test apparatus, which was outside of the cages, had two sliding trays. On each tray were two dishes with raisins, separated by translucent dividers: one for the proposer and the other for the responder (Fig. 1). Proposers would first choose one of the two trays by pulling it halfway to the cages (as far as it would go); responders could accept the offer by pulling the proposed tray the remaining distance (via the rod which came into reach only as a result of the proposer's pull) or could reject it by not pulling at all within 1 min. The responder's acceptance led to both subjects being able to reach the food in their respective dishes. Rejection led to both getting nothing, because the experimenter would remove all food dishes after the trial ended. There were four games (as in the study described above), all played within a single session: 2/8, 5/5, 8/2, and 10/0—each versus 8/2. The order of games was counterbalanced across subjects.

The most important finding is that responders tended to accept any offer. As can be seen in Fig. 2, responders rejected 8/2 offers at overall low rates (from 5 to 14% of the time). There was a trend toward different rejection rates of 8/2 offers across the four games (Friedman's χ^2_3 test = 6.643, $P = 0.069$). However, all paired comparisons were nonsignificant, indicating that, crucially, chimpanzees rejected 8/2 offers equally often regardless of the alternatives available to the proposers (27). Moreover, this trend toward rejections was in the opposite direction of the finding for humans (23). When proposers offered non-8/2 alternatives (available in all but the 8/2 game), responders accepted them differentially across the games (Friedman's χ^2_2 test = 10.00, $P = 0.012$). In line with the principle of self-interest to accept any nonzero offer, responders rejected 10/0 offers (in which the responder receives nothing) more often than 5/5 offers [Wilcoxon T^+ test = 28.00, $n = 8$ (1 tie), $P = 0.016$] and marginally more often than 2/8 offers [Wilcoxon T^+ test = 15.00, $n = 7$ (2 ties), $P = 0.063$]. Indeed, the only offers rejected by responders more than 0% of the time were 10/0 offers (one-sample t test $t_9 = 4.735$, $P = 0.001$). In short, responders did not reject unfair offers when the proposer had the option of making a fair offer; they accepted almost all nonzero offers; and they reliably rejected only offers of zero. As can be seen in Fig. 3, these results contrast strongly with those of adult humans, who reject 8/2 offers most often when a fair (5/5) option is available for the proposer and least often when the alternative for the responder is even more selfish than the 8/2 option (10/0) (23). Furthermore, unlike human responders, who report being angry when confronted with unfair offers (28), chimpanzee responders showed signs of arousal [displays and tantrums (13, 29)] in less than 2% of the test trials (all occurrences were by one individual in all trials of a single session), whereas in a previous study in which the subjects had food taken away from them, these same individuals exhibited tantrums or displays 40% of the time (21).

Consistent with previous studies on chimpanzees (19, 20), proposers did not appear to take outcomes affecting the responder into account. When given the opportunity, proposers did not make fair offers (Fig. 2) [see also (27), and fig. S1]. Given the propensity of responders to accept any nonzero offer, it is not surprising that chimpanzee proposers acted according to traditional economic models of self-interest. However, it is perhaps surprising that proposers made zero offers to the responders, given that these offers were rejected at the highest rate (Fig. 2); chimpanzees are certainly capable of distinguishing two pieces of food from zero when choosing for themselves (30).

To rule out more trivial interpretations of our results, it was necessary to demonstrate that responders and proposers understood the critical features of the task. To this end, we conducted familiarization and probe trials as well as a follow-up study. First, sensitivity to fairness in the ultimatum game requires that responders and proposers each know what the other gains. We

Fig. 2. Offers made by proposers and rejections by responders in the four games. In each game, the proposer could choose between two payoff options: 8/2 (8 raisins for the proposer and 2 for the responder) and an alternate [2/8 (2 for the proposer and 8 for the responder), 5/5 (5 for the proposer and 5 for the responder), 8/2 (8 for the proposer and 2 for the responder), and 10/0 (10 for the proposer and 0 for the responder)]. Results on the left show the total number and corresponding percentage of offers for each option made by proposers in each game. (Trials in which the proposer did not participate are not included, therefore the total number of offers varies across the games; percentages are therefore based on the total number of offers for each option out of the total number of trials played for each game.) Results on the right indicate the total number of each offer rejected and the corresponding percentage of rejections out of the total number of offers for each game.

Game	Proposer Offers	Payoffs Proposer	Payoffs Responder	Responder Rejections
5/5	39 (75%)	8	2	2 (5%)
	13 (25%)	5	5	0 (0%)
2/8	45 (87%)	8	2	3 (7%)
	7 (13%)	2	8	0 (0%)
8/2	53 (100%)	8	2	6 (11%)
		8	2	
10/0	29 (54%)	8	2	4 (14%)
	25 (46%)	10	0	11 (44%)

Fig. 3. Rejection rates (% of trials) of 8/2 offers in the four games for chimpanzees in this study (black bars) and for human participants (white bars) [data are from (23)].

therefore ran follow-up probe trials to determine whether the chimpanzees were capable of attending to the amount of food available to the partner. Subjects were tested alone, and they had to look into the distal food dishes to correctly choose the tray that would yield the largest payoff from the partner's position before going through the open door to the adjacent cage to get it. They chose correctly at greater than chance levels, demonstrating that they would have been capable of seeing payoffs to the partner (27). Second, in inhibition probe trials, we found that subjects could inhibit pulling the rod when it led to no food gain about 64% of the time, about the same rate of pulling as in the 10/0 condition, suggesting that some of the failure to reject zero offers was due, at least some of the time, to an inability to inhibit a natural tendency to pull. Third, in discrimination probe trials, responders could distinguish between all offers available to them (fig. S2), and proposers could do so for all but 10/0 versus 8/2 (fig. S1) (31), demonstrating that subjects were able to make maximizing choices.

Our subjects were from a single social group, they did not interact anonymously, and they played both roles in the game. However, anonymous one-shot games are used in experiments with humans to decrease the likelihood of making fair offers or accepting unfair offers (32, 33), and so if anything, our experimental design should have been skewed in favor of finding fairness sensitivity. The fact that chimpanzees in this study did not punish other individuals for making unfair offers may be in part a reflection of the fact that active food sharing is rare in this species (34) and may also be because they were unwilling to pay a cost to punish.

We gave chimpanzees the most widely recognized test for a sensitivity to fairness, the ultimatum game, and found that they did not systematically make fair offers to conspecifics, nor did they systematically refuse to accept unfair offers from conspecifics even though they could discriminate between the quantities available to themselves and their partners. It thus would seem that in this context, one of humans' closest living relatives behaves according to traditional economic models of self-interest, unlike humans, and that this species does not share the human sensitivity to fairness.

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Widespread Role for the Flowering-Time Regulators FCA and FPA in RNA-Mediated Chromatin Silencing

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The RRM-domain proteins FCA and FPA have previously been characterized as flowering-time regulators in *Arabidopsis*. We show that they are required for RNA-mediated chromatin silencing of a range of loci in the genome. At some target loci, FCA and FPA promote asymmetric DNA methylation, whereas at others they function in parallel to DNA methylation. Female gametophytic development and early embryonic development are particularly susceptible to malfunctions in FCA and FPA. We propose that *FCA* and *FPA* regulate chromatin silencing of single and low-copy genes and interact in a locus-dependent manner with the canonical small interfering RNA–directed DNA methylation pathway to regulate common targets.

Heterochromatin in many organisms is characterized by extensive DNA methylation and histone modifications (1). Plants display cytosine methylation in CG, CNG (N = any nucleotide), and CHH (H = A, C, or T) sequence contexts. In *Arabidopsis*, small interfering RNAs (siRNAs) are involved in localizing and maintaining these chromatin modifications in processes requiring *RNA-DEPENDENT RNA POLYMERASE2* (*RDR2*), *DICER-LIKE3* (*DCL3*), *ARGONAUTE4* (*AGO4*), and the two RNA polymerase IV isoforms, Pol IVa and b (2–9).

To identify further components required for siRNA-mediated chromatin silencing, we used a reporter system in which the *Arabidopsis* phytoene desaturase (*PDS*) gene is silenced in response to a homologous inverted repeat (*SUC-PDS*) (10). Two mutants that partially suppressed the silencing of *PDS* (Fig. 1, A, B, C, and E) showed late flowering that was reversible by vernalization. The silencing and flowering phenotypes cosegregated, and the mutations mapped to chromosomes 2 and 4. The flowering phenotype suggested involvement of *FPA* and *FCA*, two members of the autonomous pathway (11), mapping to those genomic regions. Sequencing revealed a premature termination codon in *FPA* (Trp[98]*, G to A, *fpa-8*) and *FCA* (Gln[537]*, C to T, *fca-11*). The flowering defect was confirmed by complementation analysis with previously known flowering mutants (*fca-9*, *fpa-7*, and *fve-3*; Fig. 1F), which also showed *PDS* silencing (fig. S1). Thus, *FCA* and *FPA* are required