

Numbers, not value, motivate cooperation in humans and orangutans

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Cooperation among competitors—whether sharing the burden of wind resistance in the Tour de France, forming price-fixing cartels in economic markets, or adhering to arms-control agreements in international treaties—seldom spreads in proportion to the potential benefits¹. To gain insight into the minds of uncooperative agents, economists and social psychologists have used the prisoner's dilemma task²⁻⁶ to examine factors leading to cooperation among competitors. Two types of factors have emerged in these studies: the relative rewards of defecting versus cooperating^{7,8} and breakdowns in trust, forgiveness and communication^{6,9}. The generalizability of economic and social psychological factors, however, relies on the assumption that agents' comparisons of gains and losses (whether for themselves, others, or both) preserves ratio information over arbitrary units, such as dollars and cents, and real rewards, such as food. This assumption is inconsistent with psychophysical studies on how the brain represents quantitative information, which suggests that mental magnitudes increase logarithmically with actual value¹⁰⁻¹¹. Thus, discrimination of two numerical magnitudes improves as the numerical distance between them increases¹²⁻¹⁴ and decreases as the magnitudes increase¹³⁻¹⁵. Here we show an important consequence of this representational system for economic decision making: in the prisoner's dilemma game, purely nominal increases in the *numerical* magnitude of payoffs (such as, converting dollar values to cents or whole grapes into grape-parts) has a large effect on cooperative behaviour. Moreover, a logarithmic scaling of the ratio of rewards for cooperation versus defection predicted 97% of variability in observed cooperation, whereas the objective ratio predicted 0% of variability. By linking the brain's system of representing the magnitude of rewards to motivations for cooperative behaviour, these findings suggest that the nature of numerical representations may also account for the subjective value function described by

Bernoulli²⁴, in which the apparent value of monetary incentives increases logarithmically with actual value.

To examine the effect of quantitative representations on cooperative behaviour, we manipulated nominal rewards for cooperation and observed human and nonhuman (orangutan) performance in the iterated prisoner's dilemma game. The prisoner's dilemma is defined by the payoffs two players can earn by either cooperating with their partner or defecting; specifically, the temptation for defecting when one's partner has cooperated (T, e.g. \$5) is a greater payoff than the reward for mutual cooperation (R; \$3), which in turn is greater than the punishment for mutual defection (P; \$1), which is greater than the 'sucker's reward' (S; \$0), when one has cooperated and one's partner has defected (Supplementary Figure 1). This payoff structure creates the dilemma; each individual does best on any given iteration to make the competitive move, however, overall both parties earn most if they make cooperative moves.

Assuming the prisoner's dilemma game is iterated and that one's partner is playing a reciprocal strategy, computer simulations show that players optimally maximize rewards by cooperating on all trials²; in reality, subjects cooperate considerably less often²⁵. Game theory predicts that cooperation would be avoided when the temptation to defect (T) is greater than the reward for mutual cooperation (R)⁴; in other words, when the ratio R/T is less than 1. However, since this computation is made by a living brain that, unlike computer simulations, scales numbers logarithmically^{10,11}, we predicted that cooperation would be a function of $\ln(R)/\ln(T)$.

These two functions—the linear R/T model and the logarithmic $\ln(R)/\ln(T)$ —allowed us to generate novel predictions regarding the effects of manipulating payoffs on cooperative behaviour. The linear model would predict no change in cooperation behaviour given a purely nominal change from dollars to cents ($3/5 = 300/500 = 0.6$),

whereas the logarithmic model would predict more cooperation with payoffs framed in terms of cents than in terms of dollars [$\ln(3)/\ln(5) = .68$; $\ln(300)/\ln(500) = .92$].

In Experiment 1 we conducted an iterated prisoner's dilemma task with undergraduate students in which half of the pairs were presented with payoffs in the form of dollars (R=\$3; S=\$0; T=\$5; P=\$1) and the other half with an equivalent amount of money presented in terms of cents (R=300¢; S=0¢; T=500¢; P=100¢). Contrary to the assumption made by traditional economic theory (the linear model), rates of individual cooperation, mutual cooperation, mutual defection and "forgiveness" were not equivalent in the two conditions (Figure 1). Rather, as predicted by the logarithmic model, cooperative behaviour (individual and mutual cooperation rates) was more frequent when payoffs were framed in terms of cents, whereas competitive behaviour (mutual defection) was more frequent when payoffs were framed in terms of dollars. Additionally, subjects were quicker to "forgive" their partner—that is, to cooperate after their partner's first defection—in the cents condition than in the dollars condition.

Numeric comparisons made in the prisoner's dilemma task were next examined outside the task to ensure the magnitude effect held for the numbers in the payoff matrices (e.g. \$1 vs \$5 or 100¢ vs 500¢). Consistent with our assumption, subjects ($n = 22$) more quickly compared smaller numbers (e.g. 3 vs 5) than larger numbers (e.g. 300 vs 500; $t[44] = 1.94$, $p = .03$). This difference cannot be explained by a speed/accuracy tradeoff, as subjects were equally accurate in the small number condition as in the large number condition ($t[44] = 1.82$, $p > .05$).

To ensure these condition differences were not due to subjects' simply devaluing pennies, the units (pennies) in Experiment 3 remained constant, and we either increased the payoffs by adding a constant to all matrix values (e.g. adding 100 or 1000) or decreased the payoffs by multiplying all payoffs by a constant (e.g. 0.01 or 0.001).

According to the linear model, multiplying by a constant should not change cooperation rates in relation to the baseline matrix (the “1” matrix), whereas adding a constant should lead to an increase in cooperation. However, according to the logarithmic hypothesis, adding or multiplying by a constant should lead to an increase in cooperation in relation to the baseline (Table 1).

We tested the logarithmic model by regressing R/T and $\ln(R)/\ln(T)$ against cooperation rates of subjects playing iterated prisoner’s dilemma games. While the linear model accounted for none of the variance in cooperation rates ($R^2 = 0$), our logarithmic model of cooperation accounted for virtually all of the variance ($R^2 = .97$, Figure 2). As a manipulation check, subjects were again asked to make relative size discriminations of the values in the payoff matrices used in Experiment 3. Subjects ($n = 92$) took longer to respond to very small numbers (0.003 vs 0.005) and very large numbers (1003 vs 1005) than to single digit integers (3 vs 5) ($N = 96$; $F[4, 464] = 19.12$, $p < .001$). Again, this difference cannot be explained by a speed/accuracy tradeoff, as subjects were not only faster, but more accurate in the “1” condition than the other conditions ($F[4, 464] = 3.57$, $p = .0007$).

Subjective number accounted for more variation in economic cooperation than objective number (Experiment 3) or subjective value (Experiment 1), suggesting that cognitive constraints on cooperation were more powerful than economic ones. To examine the influence of social variables on economic cooperation, we next compared performance of humans to that of a non-social primate—the orangutan (*Pongo pygmaeus*). Orangutans, like all primates, show both magnitude and distance effects²⁶. However, unlike most other primates, orangutans are solitary; the only common social pairs lasting more than a few hours among wild orangutans are mothers with their offspring²⁷. Additionally, orangutans generally perform poorly on social cognitive tasks, including imitation and theory of mind²⁸. If cooperation depends largely on social

skills, nonsocial animals such as the orangutan should not cooperate on a prisoner's dilemma task²⁹. However, if cooperation depends on representation of magnitude, orangutans should show similar patterns of cooperation to humans.

In Experiment 4 we conducted a prisoner's dilemma task with one female orangutan, Bella. In one condition she earned payoffs of whole grapes ($R=3$; $S=0$; $T=5$; $P=1$), analogous to our dollars condition in Experiment 1, and in a second condition she earned pieces of grapes such that 1 grape was cut into 10 pieces ($R=30$; $S=0$; $T=50$; $P=10$), analogous to the cents condition in Experiment 1. Contrary to the predictions of a social cognitive model, a similar pattern of results was found as with humans: on the first day of testing in the respective conditions she cooperated on 67% of the trials in the cut up grapes condition, and she never cooperated in the whole grapes condition. Like humans, she exhibited more cooperative behaviour (individual and mutual cooperation) in the grape pieces condition, and more competitive behaviour (mutual defection) in the whole grapes condition (Figure 3). Additionally, she was much quicker to forgive in the grape pieces condition than in the whole grapes condition.

As a manipulation check similar to Experiment 2, in Experiment 5 we conducted a number discrimination task with Bella and three additional orangutans. We found that the orangutans were quicker to make accurate small number discriminations ($M = 1.48$ seconds; $SD = .51$) than accurate large number discriminations ($M = 2.23$ seconds; $SD = 1.4$; Wilcoxon Signed Ranks Test; $Z = 3.36$, $p < .001$; due to the small sample size, a nonparametric test was used). Similarly, we conducted a preference task with Bella to determine whether the condition differences in cooperation could be due to preference for whole grapes as opposed to grape pieces. However, she selected grape pieces over an equivalent amount of whole grapes exactly 50% of the time. Thus, condition differences in cooperation were better predicted by numeric discrimination than by preferences for whole or cut up grapes.

We have shown that both social and non-social animals alike rely on logarithmically scaled subjective quantities when making economic decisions, suggesting that representation of number may account for variation in cooperation behaviour over and above both economic and social motives. These findings shed much light on the widely used subjective value function, famously depicted by Daniel Bernoulli's observation that "A gain of one thousand ducats is more significant to a pauper than to a rich man though both gain the same amount"²⁴. Although this function has been interpreted to suggest that differences among large rewards are less *valuable* than differences in small rewards, the function incorrectly predicted that value changes would be critical and unit changes merely nominal³⁰. Rather, it appears that nominal numeric changes in economic rewards have surprisingly robust effects on incentivizing economic cooperation, suggesting that subjective value may rely on how the brain represents numerical magnitude.

Methods Summary

In Experiment 1, two undergraduates played a prisoner's dilemma game to earn pretend money. One was instructed to play the Tit-for-Tat strategy, whereas the second received no instructions on strategy use. Payoffs varied between subjects, such that half played for dollars (R=\$3; S=\$0; T=\$5; P=\$1) and half for an equivalent amount of pennies (R=300¢; S=0¢; T=500¢; P=100¢). Experiment 2 presented subjects with a computerized reaction time task in which they were asked to quickly and accurately determine the larger of two numbers.

Procedures for Experiment 3 were identical to those of Experiments 1 and 2, except the baseline matrix (R=3¢; S=0¢; T=5¢; P=1¢) had either a constant amount added (+100, +1000) or multiplied (X0.001 or X0.01 resulting in five between-subjects conditions (Table 1).

Four orangutans from the Louisville Zoological Gardens participated in Experiments 4 and 5. Whereas humans played the prisoner's dilemma for dollars or cents, orangutans played for whole grapes or pieces, where one grape was cut into 10 pieces (whole grapes: R=3; S=0; T=5; P=1; grape pieces: R=30; S=0; T=50; P=10). The animals pursued an initial mutualism task with methodologies identical to the prisoner's dilemma except for changes to the payoff matrix intended to highlight the benefits of cooperation (whole grapes: R=5; S=1; T=6; P=3; grape pieces: R=50; S=10; T=60; P=30). Before beginning the prisoner's dilemma, orangutans were required to cooperate at 75% on two consecutive days with a human experimenter playing Tit-for-Tat. Only one orangutan (Bella) succeeded; thus, she participated in both conditions (first the grape pieces, then the whole grapes), but was required to reach criterion on the mutualism task a second time between conditions. In Experiment 5 orangutans selected which of two quantities of grapes they wanted; solution times were later coded from videos. Because of the small sample size in this experiment, nonparametric statistical analyses were used.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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The predictions made by the models for the 5 matrices in Experiment 3.

Condition	Linear Model: R/T	Logarithmic Model: ln(R)/ln(T)
"1": R = 3; S = 0; T = 5; P = 1	0.6	0.68
"0.001": R =0.003; S =0; T =0.005; P =0.001	0.6	1.10
"0.01": R =0.03; S =0; T =0.05; P =0.01	0.6	1.17
"101": R =103; S =100; T =105; P =101	0.98	1.0
"1001": R = 1003; S=1000; T =1005; P =1001	0.99	1.0

Figure 1:

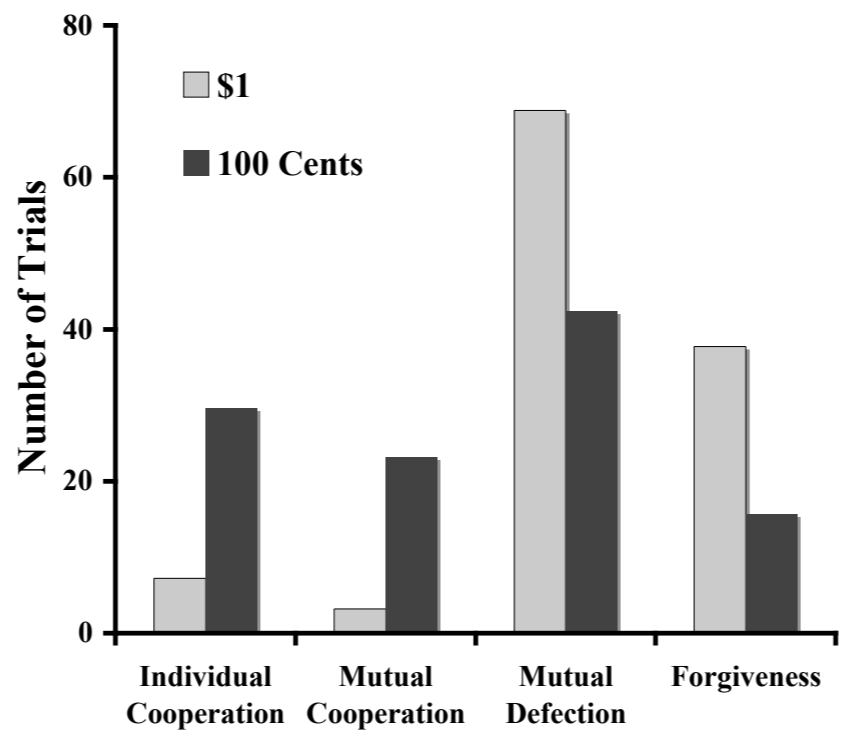
Results for Experiment 1. Subjects in the cents condition ($N = 16$) exhibited more cooperative behaviour as measured by individual ($t[29] = 2.79, p = .01$) and mutual cooperation rates ($t[29] = 2.6, p = .02$), and less competitive behaviour, as measured by mutual defection ($t[29] = 3.01, p = .01$), than subjects in the dollars condition ($N = 16$). Additionally, subjects in the cents condition were quicker to “forgive” their partner—to cooperate after their partner’s first defection—than subjects in the dollars condition ($t[29] = 1.77, p = .04$).

Figure 2:

Results for Experiment 3. The logarithmic model, $\ln(R)/\ln(T)$ accounted for virtually all of the variance in cooperation rates observed in Experiment 3 ($R^2 = 0.97$), whereas the linear model (R/T) accounted for none ($R^2 = 0$).

Figure 3:

Results for Experiment 4. As predicted, the orangutan showed similar patterns of cooperation as humans, exhibiting more individual and mutual cooperation rates, as well as less mutual defection in the cut up grapes condition as compared to the whole grapes condition. Additionally, she was quicker to forgive her partner in the cut up grapes condition than in the whole grapes condition.



- “.001”
- “.01”
- “.1”
- “.101”
- “.1001”

