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Human altruism: economic, neural, and evolutionary perspectives

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Human cooperation represents a spectacular outlier in the animal world. Unlike other creatures, humans frequently cooperate with genetically unrelated strangers, often in large groups, with people they will never meet again, and when reputation gains are small or absent. Experimental evidence and evolutionary models suggest that strong reciprocity, the behavioral propensity for altruistic punishment and altruistic rewarding, is of key importance for human cooperation. Here, we review both evidence documenting altruistic punishment and altruistic cooperation and recent brain imaging studies that combine the powerful tools of behavioral game theory with neuroimaging techniques. These studies show that mutual cooperation and the punishment of defectors activate reward related neural circuits, suggesting that evolution has endowed humans with proximate mechanisms that render altruistic behavior psychologically rewarding.

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Abbreviations

DLPFC	dorsolateral prefrontal cortex
fMRI	functional magnetic resonance imaging
PD	prisoners' dilemma game
PG	public good game

Introduction

Cooperation and sharing are commonly observed in the social life of both human and non-human societies (e.g. in foraging, usage of common pool resources, predator avoidance, territorial defense, parental care, and food sharing) [1–3]. However, human societies exhibit patterns of cooperation and a detailed division of labor that are unique in the animal world. Humans frequently cooperate with genetically unrelated individuals, even in large groups and when there are no prospects for future interactions [3]. This constitutes an evolutionary puzzle because kin selection [4], reciprocal altruism [5,6], and reputation-based models [7,8] cannot explain these patterns of cooperation. Why did human societies evolve so differently? It has been argued that humans' cognitive and emotional abilities [9•] and their capacity to establish and enforce social norms [10] are essential prerequisites for these unique patterns of cooperation. Here, we report recent evidence from economics, theoretical biology, and neuroeconomics that provide important insights into the behavioral, evolutionary, and neural bases of human cooperation. Economic experiments with humans show the importance of strong reciprocity in cooperation and the enforcement of norm abiding behavior in social dilemma situations. Research from theoretical biology investigates the evolutionary stability of strong reciprocity. Finally, recent research in neuroeconomics reveals the neural basis of human cooperation and strong reciprocity.

Capturing cooperation in the laboratory

Economists study the essence of the strategic situations underlying cooperation in the 'prisoners' dilemma game' (PD). In the PD, two players simultaneously choose between cooperation and defection. If both decide to cooperate, they both earn a high outcome (e.g. 10); if both defect, they both receive a low outcome (e.g. 5); and, if one player cooperates and the other defects, the cooperator obtains a very low outcome (e.g. 1), whereas the defector receives a very high outcome (e.g. 15). Hence, it is always better for a player to defect for any given strategy of the opponent. The PD resembles a generic cooperation dilemma in which purely selfish behavior leads to the defection of both players, even though mutual cooperation would maximize their joint payoff. Cooperation, however, is vulnerable to exploitation. The PD reflects the cooperation dilemma inherent in the provision of a public good, such as cooperative hunting or group defense, with only two individuals involved. More generally, a 'public good game' (PG) consists of an arbitrary number of players who are endowed with a certain number of tokens that they can either contribute to a project that is beneficial for the entire group (the public good) or keep for themselves. The dilemma arises from the fact that all group members profit equally from the public good, no matter whether they contributed or not, and that each player receives a lower individual profit from the tokens contributed to the public good than from the tokens kept. A purely selfish player refuses to contribute anything to the public good and free rides on the contributions of others. Hence, the public good is not provided in a group of purely selfish subjects, although provision would be in the joint interest of the group. Decades of research have gone into studying cooperation dilemma situations in controlled laboratory experiments that are designed to separate between different motives for cooperation and defection [11,12]. A considerable amount of cooperation (contributions between 40 and 60 percent of the endowment) is typically observed in PGs with one-shot interactions. However, cooperation is rarely stable if the game is played repeatedly, and deteriorates to rather low levels towards the end of the interaction period [11,12].

Cooperation enhancing behavior

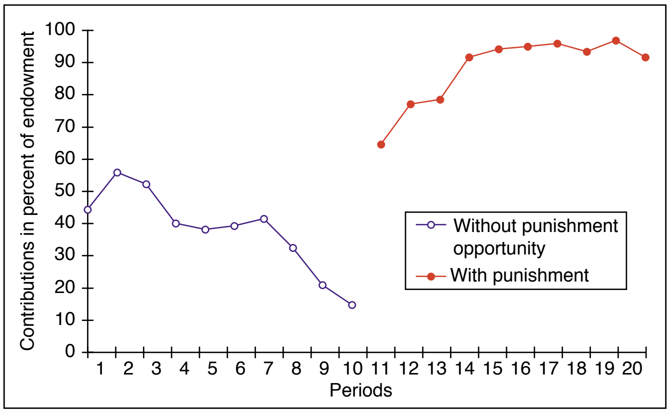
Why is cooperation observed at all and what are the mechanisms that enable and sustain human cooperation in social dilemma situations, even in an environment with (a considerable number of) selfish subjects? Recent research indicates that strong reciprocity is crucial for the establishment of cooperation in groups with a share of selfish individuals. A person who is willing to reward fair behavior and to punish unfair behavior, even though this is often quite costly and provides no material benefit for the person, is called a 'strong reciprocator' [13,14,15•]. Because strong reciprocity is costly for the individual reciprocator, the question arises as to how such behavior could evolve evolutionarily. It has been shown, however, that a positive share of strong reciprocators in the population can be part of an evolutionarily stable situation [16••,17,18].

Strong reciprocity has been observed in sequential social dilemma experiments, even in interactions with completely anonymous strangers [14,19,20], across many different cultures [21], and under stake sizes of up to three months income [22]. Strong reciprocity contributes to moderate levels of cooperation in sequential dilemma settings. If, however, effective punishment opportunities are available, high levels of cooperation are achieved because the cooperative group members can discipline selfish subjects [23,24]. In these experiments, subjects are given the possibility of reducing the other subjects' income at their own cost after having seen the others' contribution to the public good. These punishment possibilities are heavily used, and the lower an individual's contribution relative to the group average, the more the individual is punished. As a result, a large increase in cooperation is observed (see Figure 1). Punishment in this experiment could, in principle, be attributed to selfish incentives because of repeated interactions between the subjects. The absence of any material gain from punishment is ensured in the study by Fehr and Gächter [25], because the punished and the punishing subjects never interact again. Nevertheless, punishment is frequently observed, and punished subjects typically increase their cooperation in future interactions with other subjects, so the future interaction partners of the punished subjects benefit from the punishment. Recent evolutionary models show that altruistic punishment even survives evolutionary pressures in relatively large groups [16••,18].

Conditional cooperation

The recent literature distinguishes between strong negative reciprocity, for example the punishment of free

Figure 1



The impact of punishment opportunities on human cooperation. Fehr and Gächter [23] studied the impact of punishment opportunities on cooperation rates in a public goods experiment. The figure shows subjects' average contributions to the public good (as a percentage of their endowment) over time. During the first ten periods, no punishment was possible. During periods 11–20, group members could punish each other after they observed each member's contribution level, but punishment was also costly for the punisher. At the beginning of the first ten periods cooperation rates of roughly 50% of the endowment were observed, but cooperation unraveled over time. The majority of subjects contributed nothing to the public good in period ten, and the rest contributed little. In period 11, the subjects were informed that a new experiment would start in which they would have the opportunity to punish the other group members at a cost to themselves. The punishment opportunity immediately increased cooperation levels to 65% of the endowment. Moreover, over time cooperation rose dramatically, until almost full cooperation was attained.

riders, and strong positive reciprocity, which takes the form of 'conditional cooperation' [26,27]. Conditional cooperation means that a subject increases his or her contributions to a public good if he or she expects that other subjects will also raise their contributions. The existence of conditional cooperators renders the subjects' beliefs about other subjects' behavior important. These beliefs can be based on past behavior in a repeated interaction [27] but they can also be based on the knowledge that the members of the interacting group are 'alike'. In recent experiments [28], subjects are ranked with respect to their contribution in a one-shot PG game and than sorted into groups of individuals with similar ranks. Cooperation in these newly composed groups of like-minded people (with respect to cooperation) is significantly higher than under the control situation of random group composition. Similar results are found when the interacting groups are not exogenously determined but endogenously composed with respect to the stated preferences of the participants (Page T, Putterman L, Unel B, unpublished, available at http://www.econ.brown.edu/fac/Louis_Putterman/working/pdfs/wp2002-19.pdf).

The instances in real-life situations in which someone can directly select the partners with whom to interact in a social dilemma situation are limited (e.g. spouses, employees). In some cases, it is only possible to select the rules that govern the interaction, but not the concrete partners themselves (e.g. corporate culture, political regime). Recently, a repeated public good situation was studied in which each subject chooses at the beginning of each round whether he or she wants to interact in a regime with costly punishment possibilities after having seen the contributions of the others, or to participate in a regime without any sanctioning options. A subject then interacts with all other subjects that chose the same regime in that round (Gürerk Ö, Irlenbusch B, Rockenbach B, unpublished). Two remarkable results could be observed. Initially, about two-thirds of the subjects decided to interact under the regime without a punishment possibility, but the proportion of the subjects in this regime steadily decreased with time, leading to almost complete extinction towards the end of the experiment. The subjects that voluntarily chose to interact in the regime that allows for punishment heavily punished free riders and achieved almost full cooperation. This cooperation was stable even when the interacting group became rather large (because almost all subjects had since joined this group) and the experiment approached its end (Figure 2a). The contribution levels in the punishment institution were significantly lower in a control treatment in which the experimenter exogenously allocated the subjects to the two regimes (Figure 2b). Interestingly, a choice between a regime that allows costly rewarding of other subjects after having seen their contributions and a baseline regime without any sanctioning or rewarding technology does not lead to such clear results (Figure 2d). A decay of cooperation over time is observed in both situations and subjects move back and forth between the two regimes, with about 70 percent of the subjects ending up in the reward regime.

Although the punishment of free riders in PGs is a very effective cooperation device, the conclusion that (the threat of) punishment is always an adequate and successful instrument for governing social interactions is wrong. The threat of punishment can have detrimental effects on cooperation in sequential social dilemmas if the punishment is not used to enforce a socially beneficial outcome but instead is applied to enforce a higher material payoff for the punisher (Figure 3; [29]). This indicates that punishment is only powerful for enhancing cooperation if it is 'socially justified'.

Third-party punishment

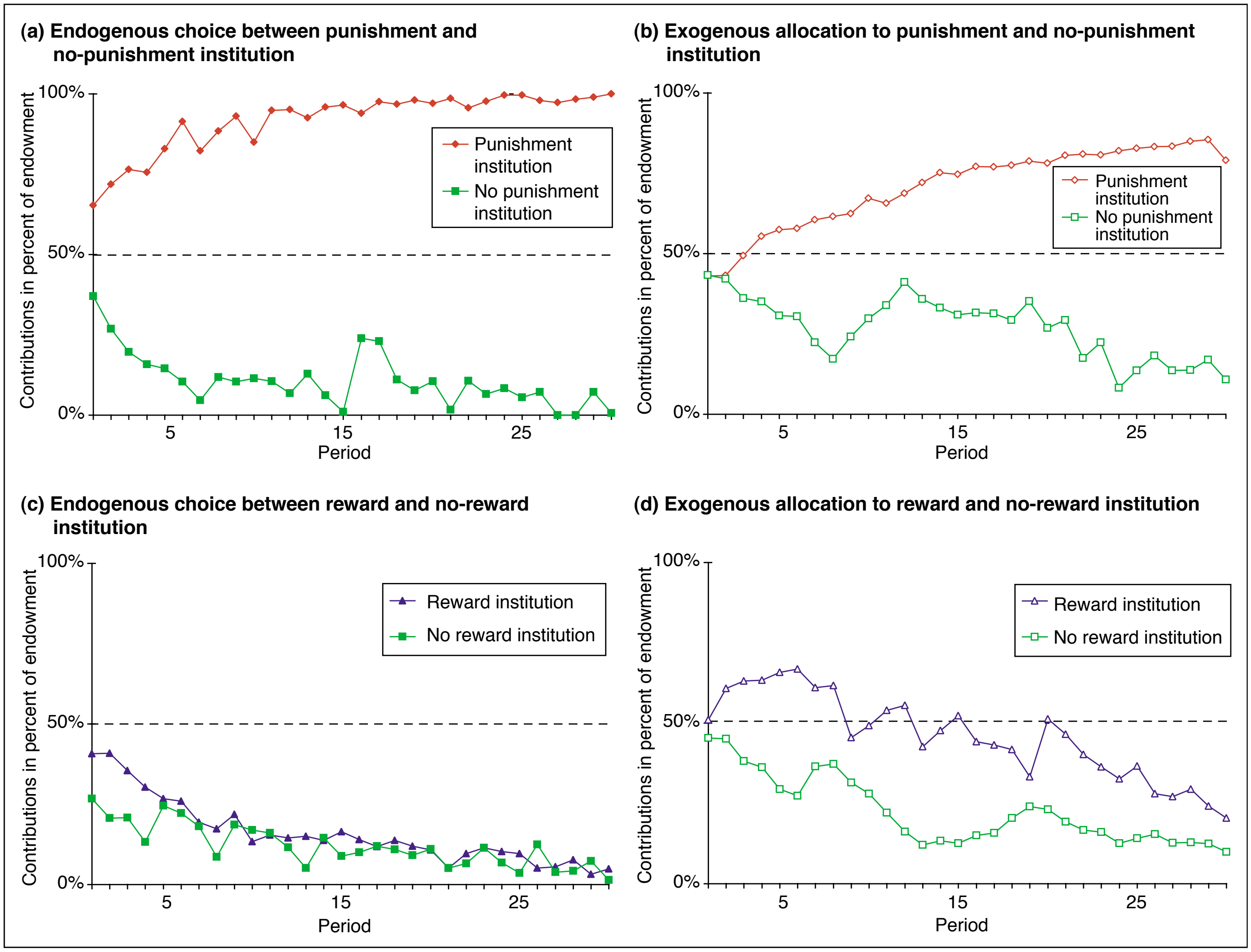
The PG experiments have shown that subjects are willing to sacrifice money to enforce cooperation in their group. However, a key element in the enforcement of many social norms is that people punish norm violators not for what they did to the punisher but for what they did to others [30,31]. In a 'third-party punishment' game [32•], an allocator is endowed with a sum of money and may give a share of it to a recipient who has no endowment. A third party that is endowed with a smaller sum of money observes this allocation and can then spend money to punish the allocator. Because it is costly to punish, no selfish third party will ever punish. Yet, if a fairness norm applies to the situation, punishers are expected to punish unfair transfers. In fact, 55 percent of the third parties punish the allocator for transfers below 50 percent; the lower the transfer, the higher the punishment. Moreover, between 70 and 80 percent of the recipients expect that allocators will be punished for unfairly low transfers.

Neuroeconomics

What are the proximate mechanisms behind strong reciprocity? Recent neuroeconomic studies that scan subjects' brains while they are making decisions in interactive economic experiments provide interesting results on the neural foundations of strong reciprocity [33–35,36••,37••]. They support the hypothesis that neural representations of emotional states guide human decision-making and they suggest that subjects derive specific rewards from mutual cooperation and the punishment of norm violators.

A recent study [36••] demonstrated the importance of the interplay of emotions and cognition in economic decision-making. Nineteen participants who responded to fair and unfair offers in a bargaining game were scanned using functional magnetic resonance imaging (fMRI). Less fair offers activated the bilateral insula, which has been implicated in negative emotional states such as disgust, pain, hunger, and thirst. Subjects with stronger insula

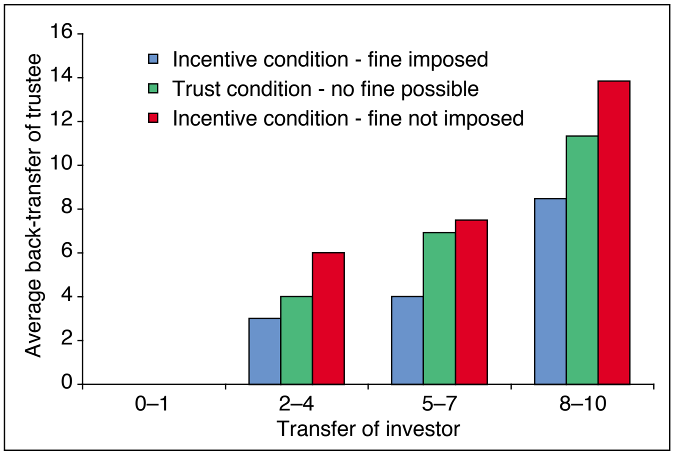
Figure 2



The impact of endogenous institution selection on human cooperation. Gürerk, Irlenbusch, and Rockenbach (unpublished) studied the impact of endogenous institution choice on the level of public good provision. Panels **(a–d)** display the average contribution levels during the 30 periods of the experiment in the four different treatments. (a) In this treatment each player could freely choose to join either the punishment or the no-punishment institution at the beginning of each round. After subjects joined an institution, they played a public good game with those subjects who had also joined that institution. Subjects in the punishment institution could punish the other members of the institution at a cost to themselves after they were informed about others' contributions. Neither a rewarding nor a punishment of others was possible in the no-punishment institution. (c) In this treatment, the players could choose to join either the reward or the no-reward institution. Subjects in the reward institution could reward other members of that institution at a cost to themselves after they were informed about others' contributions. Neither a rewarding nor a punishment of others was possible in the no-reward institution and it was hence identical to the no-punishment institution. In the treatments (b) and (c) the experimenter exogenously allocated the subjects to the different institutions at the beginning of the experiment and the subjects were not able to switch between institutions. The figure shows that the contribution levels are highest in the punishment institutions of (a) and (b). In all other institutions cooperation unravels over time. If subjects have the possibility to select endogenously the institution (panel a) contributions reach almost 100% of the players' endowment in the punishment institution and remain stable even towards the end of the interaction period. It is remarkable that the voluntary choice of a punishment regime leads to higher cooperation levels than an exogenous allocation to that institution (panel b).

activation to unfair offers were also more likely to reject these offers. Unfair offers from a human partner also caused stronger insula activation than unfair offers from a computer partner, which suggests the importance of the social context for the insula activation. Unfair offers also activated the dorsolateral prefrontal cortex (DLPFC) and the anterior cingulate cortex (ACC). These activations are interesting because the DLPFC is a region that is often associated with goal maintenance and executive control and the ACC has been implicated in detection of cognitive conflict. In fact, if the insula activation to unfair offers was stronger than the DLPFC activation subjects tended to reject the offer, whereas subjects tended to accept an unfair offer if the DLPFC activation was stronger.

Figure 3



The impact of unfair sanctioning threats on altruistic cooperation. Fehr and Rockenbach [29] conducted a version of a sequential one-shot PD. In this game one player, we call him A, has to move first by making a more or less cooperative choice. Player A also announces how much the other player, we call him B, should cooperate. Then player B is informed about A's degree of cooperation and A's desire, upon which B chooses how much to cooperate. The rules of the game ensure that both players maximize their joint payoff if they both cooperate maximally. However, player B has a strong selfish temptation to choose minimal cooperation because cooperation is costly for him. Any positive cooperation level of B is, therefore, an altruistic act. Fehr and Rockenbach implemented two treatment conditions. In the 'trust condition', player A cannot threaten to punish player B. In the 'incentive condition' player A can threaten to punish B but A can also voluntarily refrain from imposing a threat on B. This figure shows B's cooperation as a function of A's cooperation level. B cooperates more in response to higher cooperation levels of A in all conditions. However, the figure also shows that B's cooperation is highest if A could have chosen a punishment threat but voluntarily refrained from doing so. B's cooperation is lowest if A threatens B. Detailed analysis showed that A's punishment threat undermined B's altruistic cooperation if the threat was associated with unfairly high desired cooperation levels.

fMRI analysis of subjects playing a PD indicates that mutual cooperation with a human partner yields stronger activation of the brain's reward circuit (components of the mesolimbic dopamine system including the striatum and the orbitofrontal cortex) than mutual cooperation with a computer partner that yields the same monetary payoff does [34]. Moreover, there is also evidence implying a negative response of the dopamine system if a subject cooperates but the opponent defects. These findings indicate that there is a neural basis for strong reciprocity. This interpretation receives further support from an imaging study that scanned subjects while they were making gender judgments of faces that were previously attached to opponent players in a sequentially played PD [38••]. Some faces were associated with cooperative decisions, some with defections, and some were neutral. The study shows that the presentation of faces of intentional cooperators caused increased activity in left amygdala, bilateral insula, fusiform gyrus, superior temporal sulcus, and reward-related areas. Moreover, a particularly noteworthy result is that merely seeing cooperators' faces during the gender judgment task activated reward-related areas.

One of the major puzzles posed by the existence of strong reciprocity is the fact that many cooperative subjects punish defectors in one-shot PD games although punishing is also costly for punisher. A new study that combines a sequential PD experiment with positron emission tomography (PET) provides a solution to this puzzle. A punishment opportunity augmented the PD in this study because the cooperating player could punish a defecting player. In the effective punishment condition the cooperator could reduce the defector's economic payoff by punishing him, whereas the cooperator could only punish the defector symbolically in a control condition, that is, the assignment of punishment points to the defector did not reduce the defector's payoff in this condition. The contrast between the effective and the symbolic punishment condition activated the dorsal striatum, which is well known for its reward processing properties. The study also shows that those subjects with a higher activation in the dorsal striatum impose a greater punishment on defectors. Moreover, additional analyses suggest that the activation in the dorsal striatum reflects the anticipated satisfaction associated with the punishment.

The previous results indicate a neural basis for certain forms of strong reciprocity. However, we do not know at present the neural basis of third-party punishment [32•], which plausibly requires empathizing with the victims of norm violations. A study in which the brain activity of humans experiencing pain was compared to the brain activity of humans observing a loved one experiencing a similar pain stimulus [39] reveals that empathy with the pain of others does not activate the whole pain matrix, but is based on the activation of areas that represent solely the affective dimension of pain. This observation yields the neural basis of empathy (between loved ones). Hence, an interesting question is whether the same brain areas are activated in third party punishment, that is, when people empathize with strangers who became the victim of a norm violation.

Conclusions

Economic experiments show that strong reciprocity is a key force in human cooperation, and evolutionary models indicate that it can be a stable and adaptive trait. In addition, neuroeconomic studies examined the neural basis of strong reciprocity. The anterior insula seems to play a crucial part in the willingness to reject unfair outcomes, and reward-related circuits involving the ventral and dorsal striatum seem to be important for human cooperation and the punishment of norm violations. These exciting results suggest that the combination of interactive economic experiments with brain imaging techniques constitutes a fertile area for future research that promises a better understanding of complex social behaviors that form the basis of human societies.

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This study documents the role of altruistic third party punishment in the enforcement of fairness and cooperation norms. It is shown that many humans punish the violation of fairness and cooperation norms. However, punishment by third (unaffected) parties is shown to be significantly weaker than punishment of second parties (whose payoff is reduced by the norm violation).

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Why do many humans punish norm violators although the act of sanctioning is costly for them and yields no economic rewards? This study suggests that evolution has endowed humans with a proximate mechanism that renders punishment of norm violators psychologically rewarding. The authors test this hypothesis by combining PET with a sequential PD with a sanctioning opportunity. It is shown that the sanctioning of defectors activates reward related brain areas such as the dorsal striatum. Furthermore, the data suggest that the activation in the dorsal striatum reflects the expected satisfaction from punishing.

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Why do many humans cooperate in the one-shot PD although it is in their economic self-interest to defect? The results of this study suggest that mutual cooperation provides peculiar psychological benefits that could explain why subjects prefer mutual cooperation over unilateral defection. The study shows that merely seeing the face of an individual that previously cooperated in a one-shot PD activates reward related neural circuits. Previous work by Rilling *et al*. [34] also suggests that mutual cooperation is associated with hedonic rewards that go beyond the mere fact that subjects earn money. However, the results of Rilling *et al*. are based on a repeated PD, in which mutual cooperation can be in the economic self-interest of a subject, whereas these results are based on a one-shot dilemma, in which mutual cooperation is never in the economic self-interest of a player. The activation of reward related brain areas in a one-shot PD is, therefore, cleaner evidence for the hypothesis that the reward value of mutual cooperation exceeds the reward value of the economic payoff that is associated with mutual cooperation.

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