Disrupting the prefrontal cortex diminishes the human ability to build a good reputation

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Reputation formation pervades human social life. In fact, many people go to great lengths to acquire a good reputation, even though building a good reputation is costly in many cases. Little is known about the neural underpinnings of this important social mechanism, however. In the present study, we show that disruption of the right, but not the left, lateral prefrontal cortex (PFC) with low-frequency repetitive transcranial magnetic stimulation (rTMS) diminishes subjects' ability to build a favorable reputation. This effect occurs even though subjects' ability to behave altruistically in the absence of reputation incentives remains intact, and even though they are still able to recognize both the fairness standards necessary for acquiring and the future benefits of a good reputation. Thus, subjects with a disrupted right lateral PFC no longer seem to be able to resist the temptation to defect, even though they know that this has detrimental effects on their future reputation. This suggests an important dissociation between the knowledge about one's own best interests and the ability to act accordingly in social contexts. These results link findings on the neural underpinnings of self-control and temptation with the study of human social behavior, and they may help explain why reputation formation remains less prominent in most other species with less developed prefrontal cortices.

decision making | social interaction | transcranial magnetic stimulation

Humans are unique in the extent to which social norms regulate their lives, and reputation formation is a powerful mechanism in generating norm compliance. "Reputation is what you are in the light; character is what you are in the dark," says a Chinese proverb. In other words, although much norm compliance is voluntary, there is ample evidence that people are more likely to comply with norms when they feel observed by others. In such a situation ("in the light"), individuals signal their quality as cooperators to future interaction partners, thereby forming a good reputation.

Reputation formation is characterized by 2 features. First, the signals for building a good reputation (in human societies) are costly in many cases; otherwise they would be "cheap talk" and thus of no informational value for the potential interaction partner. Second, this process of costly reputation formation is characterized by a trade-off between the current benefits of defection and the future benefits of a good reputation.

Evidence for the crucial role of a good reputation in social decision making comes from empirical studies showing that individuals increase their levels of cooperation and are more likely to comply with norms when they know that others observe their behavior, and that individuals cooperate with those whom they observe cooperating with others (1–16). Thus, the concern for reputation profoundly affects our daily social interactions and motivates many important decisions in our lives.

Although reputation formation mechanisms are ubiquitous in social exchange, their neurobiological substrate remains largely unknown. Moreover, a universal question arises, one with relevance not only to cognitive neuroscience, but also to fields of research in evolutionary biology, developmental psychology, and behavioral economics: Which skills are required to acquire a good reputation? Intuitively, we assume that there must be a self-control capacity, because forming a reputation typically requires an individual to overcome the temptation to defect to gain future reputation benefits. From a neurobiological perspective, we thus assume the involvement of the PFC, because this region has been shown to be involved in self-control processes (17–19).

Four previous neuroimaging studies have examined reputation (20–23). Two of these studies did not address the neural underpinnings of the process of individual reputation formation; that is, they did not focus on the individual who forms a reputation. Instead, they examined individuals who made decisions based on reputation information about another individual (20, 21). In one of these studies, for example, subjects played iterative trust games with 3 partners whose (fictional) profiles make them seem morally good, bad, or neutral (21). The study found that information about the interaction partner's moral reputation affected the investors' reward prediction error signal in the caudate nucleus during reciprocal exchange. Another study showed activation of reward-related brain areas when a subject learned that others perceived his or her reputation as good (22). Finally, one study that used hyperscanning functional MRI (fMRI) while 2 interacting partners played an iterated trust game showed that the peak activation of the caudate nucleus underwent a temporal shift as the reputation of the interaction partner developed (23).

No previous study provides causal evidence about the brain processes involved in costly reputation formation, however. Functional imaging methods, although indispensable, do not permit causal inferences about the effect of brain processes on human behavior, because the observed neural activations could be spuriously correlated with task performance and need not necessarily play a causal role in task execution (24, 25). In contrast, brain stimulation techniques, such as transcranial magnetic stimulation (TMS), interfere noninvasively with the activity of defined areas in the human cortex, allowing researchers to observe the behavioral impact of an increase or decrease in the cortical excitability of the stimulated brain region. Application of low-frequency repetitive TMS (rTMS) for several minutes leads to suppression of activity in the stimulated brain region that outlasts the duration of the rTMS train by about half the duration of the stimulation (26, 27). Here we investigated the effect of disrupting the PFC by means of rTMS on subjects' reputation formation.

We chose a version of the trust game (Fig. 1*A*) as a vehicle for investigating the effects of rTMS on costly reputation formation.

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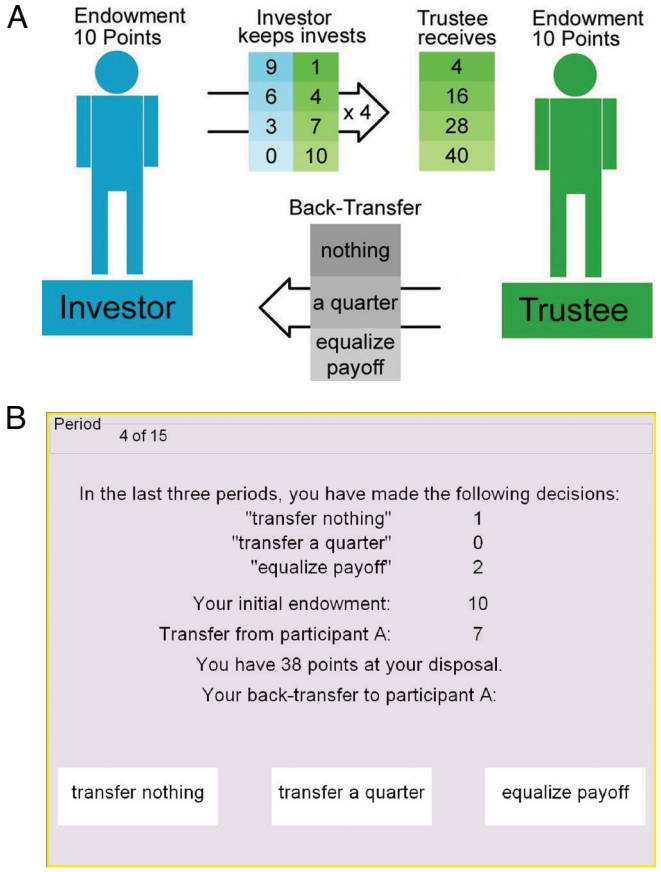

Fig. 1. (*A*) Schematic representation of the task: design of one period of the trust game. In each period, 2 anonymous individuals, a first mover (investor) and a second mover (trustee), receive an endowment of 10 points each. The investor must decide how many points he wants to transfer to the trustee. The experimenter quadruples the invested points and transfers them to the trustee, who then decides how many points he would like to back-transfer to the investor. To reduce the game's cognitive complexity, the strategy space was limited for both the investor and the trustee. The investor could transfer 1, 4, 7, or 10 points (1 point equals 0.20 CHF, which was about 0.18 US$ at the time the experiment was conducted), and the trustee had 3 options: he could back-transfer nothing, a quarter of the received amount, or an amount that equalized the period payoff between the investor and the trustee. The latter restriction also has the added advantage that the reputational implications of different trustee behaviors are transparent. For example, paying back nothing is unambiguously bad for the formation of a good reputation, while equalizing payoffs is unambiguously good. (*B*) Trustee's decision screen. On the top section of the screen, the trustee can see his decisions in the 3 previous periods. The information about past decisions is not in chronological order. In the reputation condition, the trustee also knows that in this condition, the investor is informed about the trustee's previous 3 decisions before he makes a transfer decision. Thus, the trustee knows that the investor can condition his transfer on the trustee's previous 3 back-transfer decisions. This also means that the trustee's back-transfer in the current period affects the information that future investors receive about him; that is, it affects his reputation in future periods. The trustee's decision screen also contains information about the current investor's transfer and the resulting points at the trustee's disposal, in the middle section of the screen. The bottom section features 3 clickable buttons for the trustee's decision.

Subjects played 15 periods of this trust game with randomly rematched partners each period [see supporting information (SI) *Materials and Methods*].

We implemented 2 treatment conditions, which we term an "anonymous condition" and a "reputation condition." In the anonymous condition, the trustee's previous decisions are unknown to the current investor, while the investor has information

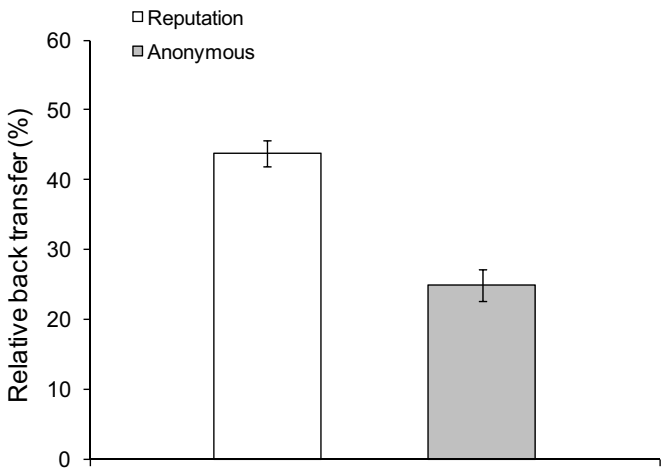

Fig. 2. Trustees' behavioral responses. Comparison of mean of back-transfer in the reputation condition versus the anonymous condition; data pooled over all stimulation groups.

about the trustee in the reputation condition (Fig. 1*B*). He can observe the trustee's decisions in the previous 3 periods (ie, how many times the trustee chose to back-transfer "nothing," to back-transfer "a quarter," or to "equalize payoff"). Thus, a trustee is likely to acquire a bad reputation by choosing to back-transfer "nothing," whereas a trustee improves his reputation by choosing to "equalize payoff." Because a trustee who transfers nothing is unlikely to receive high transfers from the investors in future periods, the trustees have an incentive to make relatively high back-transfers in the reputation condition. Thus, this reputation incentive generates a motivational conflict for the trustees. A trustee could maximize his short-run self-interest by choosing to transfer nothing back to the investor in the current period, but this action is likely to have detrimental effects for his reputation and decreases future investors' willingness to transfer money to him. Therefore, to reap the benefits from a good reputation in future periods, a trustee must constrain his immediate self-interest and forgo the current option of back-transferring nothing.

In contrast, the strategic incentive for behaving in a cooperative manner is completely absent in the anonymous condition because the investors have no information about the trustees' past behavior. In terms of the Chinese proverb cited at the beginning of this paper, the trustees in the anonymous condition act in perfect darkness, and only their "character" plays a role. Thus, the anonymous condition measures how much the trustee is willing to return voluntarily to the investor (which may be viewed as a form of altruistic behavior). This amount reflects the trustee's preference for back-transfers if there are no strategic reputation incentives. Consequently, if the trustee returns amount x to the investor in the anonymous condition, then the trustee is apparently not willing to return more than x. However, the trustee very well might return more than x in the reputation condition, as strategic incentives for reputation formation are then present; that is, in his case the trustee must override his immediate self-interest to build a good reputation.

How will disruption of the PFC with low-frequency rTMS affect the trustees' behavior? Because the lateral PFC has been shown to be reliably involved in overriding prepotent responses and self-control processes (17–19), and because costly reputation formation requires overriding immediate benefits, disrupting this brain region should functionally weaken self-control capacity and thus lead to a lower back-transfer in the reputation condition compared with the other stimulation groups. In con-

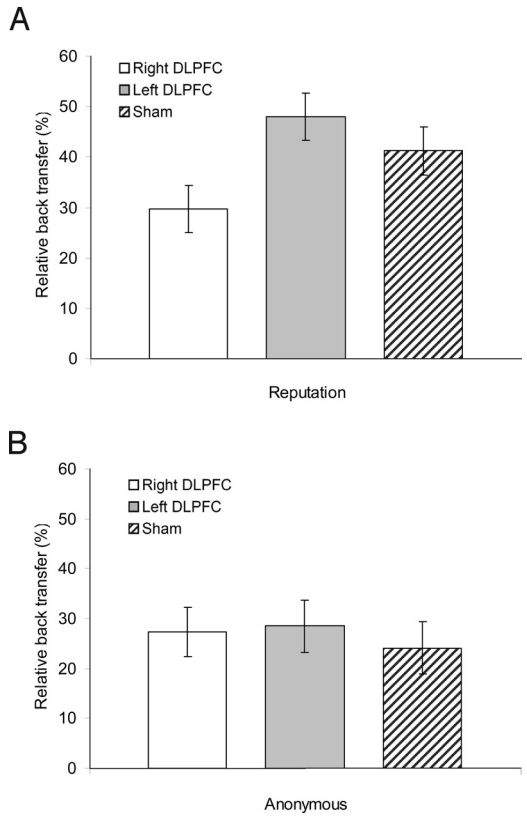

Fig. 3. Trustee's behavioral responses across stimulation conditions. (*A*) Mean back-transfer associated with the investor's highest investment in the reputation condition. Subjects whose right DLPFC was disrupted back-transferred significantly less points than those in the other 2 stimulation groups ($P < .02$). (*B*) Mean back-transfer associated with the investor's highest investment in the anonymous condition.

trast, little or no self-control effort is involved in the anonymous condition, because the trustee has no reputational incentive to back-transfer more than his immediate preference dictates. Therefore, we would expect to see little difference between the stimulation groups for the anonymous condition. Moreover, because the right lateral PFC in particular has been shown to be involved in control capacities (17, 19), we hypothesized that disruption of the right, but not the left, lateral PFC will lead to difficulty resisting the temptation to go for the immediate benefit and thus reduce the ability to form a good reputation.

It is important to note that the trustee in the reputation condition knows that the investor has information only about his 3 previous choices (i.e., "nothing," "a quarter," or "equalize payoff"), not about how high the corresponding previous investors' investments were in the previous 3 periods. For example, if a trustee receives an investment of 1 point and chooses "equalize payoff" to form a good reputation, then he actually back-transfers 2.5 points. This is because he in fact received 4 points (1 point, quadrupled by the experimenter), and back-transferring 2.5 of those 4 points together with the initial endowment of 10 points leaves both the investor and the trustee with equal amounts totaling 11.5 points. If a trustee receives an investment of 10 points and chooses "equalize payoff," then his back-transfer is 25 points, and both players end up with a total of 25 points. Because future investors will observe only the choice "equalize payoff," not the amount actually transferred by the investor, the trustee's reputational benefit is the same in both cases. The immediate costs, however, are different: 2.5 points in the first case and 25 points in the second case. Therefore, the costs of reputation formation (ie, the number of points the trustee must forego to form a good reputation) vary with the size of the investment, while the effect of a particular choice on a trustee's reputation is always the same, regardless of the received investment. In other words, while the future reputational value of a trustee's choice is independent of the investor's investments, the immediate cost of reputation formation, and thus the temptation to maximize one's short-run self-interest, varies with the size of the investment. Thus, the self-control effort necessary to constrain short-run self-interest is likely to be much higher in cases of a large investment compared with a small investment, where reputation formation is almost costless. This variation in the temptation to maximize one's short-run self-interest by paying back nothing enables us to investigate whether the effect of disrupting the lateral PFC depends on the degree of self-control required for reputation formation.

This feature of our design puts important constraints on the interpretation of a possible effect of right lateral PFC disruption. If, for example, rTMS of the right PFC primarily reduced the trustees' back-transfers in the reputation condition at low investment levels, then an interpretation of this effect in terms of reduced self-control abilities would be less convincing, because little temptation to defect exists at low investment levels. However, if rTMS primarily affected their back-transfers at high investment levels where the temptation to defect is high, then an interpretation in terms of reduced self-control would make a lot of sense. To examine whether lateral PFC activity is a crucial factor in the trustees' reputation formation, we applied low-frequency rTMS over the dorsolateral prefrontal cortex (DLPFC) for 15 min to healthy subjects in the role of the responder (see *Materials and Methods*).

Results

Our results show that reputation formation paid off for the trustees in the long run, because investors gave more points to trustees who cooperated in the past than to defectors. Trustees had a 71% probability of receiving a 10-point investment if they always equalized payoffs, dropping to $< 6\%$ if they always chose to back-transfer nothing. Consequently, a strategy of cooperating in the first 14 periods and defecting in the last period (i.e., rational cooperation) was on average 43% more profitable (371 points) than always defecting (260 points). Thus, the trustees had an incentive to constrain their short-run self-interest and to back-transfer a high amount in the reputation condition, because the investors conditioned their investments on the trustee's past actions. Accordingly, our results show that trustees cared greatly about their reputation when reputation formation was possible. Subjects sent back on average 24.9% of the transferred amount in the anonymous condition, compared with 43.8% in the reputation condition (Fig. 2).

Of primary interest are back-transfers with regard to the investors' highest investment, because the temptation to follow short-run self-interest, and thus the requirement for self-control effort, is greatest in this case. Focusing on the reputation condition (Fig. 3*A*), we see that the back-transfer for the highest investment was 41.2% following sham rTMS and 48.0% after real rTMS of the left DLPFC. These results contrast sharply with the back-transfer of 29.7% after rTMS of the right DLPFC. The differences in back-transfers across the stimulation groups are significant in the reputation condition [generalized least squares (GLS) regression, $P < .001$ for the difference between right and left DLPFC and $P = .015$ for the difference between right DLPFC and sham condition; see SI *Materials and Methods* for details]. In contrast, we found no significant differences in back-transfers among the 3 stimulation groups in the anonymous condition (GLS regression, $P = .816$ for the difference between right and left DLPFC and $P = .232$ for the difference between right DLPFC and sham) (Fig. 3*B*).

In other words, while disruption of the right DLPFC significantly reduced back-transfers in the reputation condition in cases of highest investment, it did not do so in the anonymous condition. This indicates a significant differential effect of rTMS across stimulations (right DLPFC, left DLPFC, sham) in the reputation condition, but not in the anonymous condition. See SI *Materials and Methods* for additional statistical analyses.

Interestingly, those subjects in the reputation condition who received rTMS to the right DLPFC transferred similar amounts back to the investor as those in the anonymous condition (compare Fig. 3*A* and 3*B*; $P = 0.667$; *t* test). Thus, disrupting the right DLPFC completely removed the behavioral impact of the reputation condition, but had no effect on behavior when reputation formation was not possible. Moreover, there were no significant differences across stimulation groups for lower investments, where the temptation to yield to short-run gains and thus the recruitment of self-control effort was lower (all $P >$ .193).

rTMS of the right DLPFC limited subjects' ability to override immediate short-run benefits. However, rTMS changed neither subjects' perception of the prevailing fairness norm nor their ability to assess the consequences of past and current trustee behaviors on future investments, which we elicited immediately after the experiment (see *Materials and Methods*). First, subjects in all 3 stimulation groups judged the scenario of back-transferring nothing in response to an investment of 7 as rather unfair, and there were no differences in fairness judgments across groups ($P = .376$ Kruskal-Wallis test). Second, rTMS of the right DLPFC did not change subjects' ability to assess the consequences of past and current trustee behaviors, because subjects in the different stimulation groups predicted the same investments by future investors in response to a given profile of past back-transfers ($P = .950$; Kruskal-Wallis test). Moreover, if rTMS of the right DLPFC had impaired subjects' general ability to perform complex calculations, then we would have observed differences across stimulation groups for the lower investments as well; however, our results show a behavioral effect only for the highest investments. This indicates that disruption of the right DLPFC had an effect on the *behavioral* ability to form a good reputation, even though it did not affect subjects' ability to perform complex cognitive operations, their recognition of the prevailing fairness norm, or their ability to assess the future consequences of back-transfer behaviors.

We also investigated whether individual differences in impulsivity and the propensity to reciprocate kind or hostile acts can explain our results. We found that neither dispositional differences in subjects' reciprocity norm nor individual differences in impulsivity across treatment groups can explain the behavioral differences across conditions; there was no difference across treatments for impulsivity [Behavioral Inhibition System (BIS) scale: $P = .827$; Behavioral Approach System (BAS) scale: $P = .967$; Kruskal-Wallis test] or for the reciprocity norm (positive reciprocity scale: $P = .741$, negative reciprocity scale: $P = .971$; Kruskal-Wallis test).

Discussion

Our results indicate a highly specific, lateralized effect of a disrupted function of the lateral PFC on the ability to form a reputation for being trustworthy. We found no differences between the stimulation groups in the anonymous condition, where the incentives for reputation formation are absent. In this condition, only subjects' preferences for altruistic behaviors can induce them to repay trust, implying that an interference with the function of the right lateral PFC leaves their altruistic propensities to behave in a trustworthy manner unchanged. This contrasts with an rTMS effect in those circumstances in which costly reputation formation requires a particularly strong recruitment of self-control effort, that is, when the investors make a high investment. In this situation, the incentive to yield to the short-run costs for building a reputation is greatest, suggesting an interpretation of the rTMS effect in terms of the reduced ability to recruit the required self-control resources. The absence of any rTMS effect on subjects' ability to recognize the prevailing fairness norm supports this conjecture. Thus, despite the fact that subjects are well aware of the existing fairness norm, and even though they have pecuniary incentives to obey this norm in the reputation condition, they nevertheless do not do so, suggesting that rTMS causes a specific inability to constrain short-run temptations, rather than a cognitive inability to perceive the normative demands involved in the situation. The finding that rTMS had no effect on subjects' ability to assess the future consequences of past back-transfers further supports our interpretation. Subjects across all 3 stimulation conditions had the same knowledge about the future benefits of high current back-transfers, but only those subjects with transiently disrupted right DLPFC function were less able to constrain their short-run self-interest and thus exploit this knowledge.

Taken together, these results support the hypothesis that right, but not left, lateral PFC activity is a crucial factor in the ability to forego immediate benefits to form a good reputation. Subjects whose right lateral PFC was disrupted behaved as if they were not concerned about their reputation when reputation formation required forgoing a large current benefit, suggesting that they were less able to pay an immediate cost for future social reputation benefits even though their ability to assess these benefits cognitively remained intact. These findings suggest an important dissociation at the neurobiological level between the knowledge about what is in one's own best interests in social interaction situations and the ability to act accordingly. Moreover, by providing causal evidence on the role of the prefrontal cortex in costly reputation formation, our findings also may help explain why reputation mechanisms are rare in other species with less-developed prefrontal regions. In highly complex processes such as reputation formation, brain areas do not act in isolation, but rather must work together as a network. Future studies could combine low-frequency rTMS and fMRI to explore how different brain regions interact on the functional-anatomical level in reputation formation.

Materials and Methods

Transcranial Magnetic Stimulation. We applied low-frequency rTMS for 15 min to 87 healthy subjects acting in the role of the trustee (see SI *Materials and Methods* for more details). To investigate a possible hemispheric laterality in the role of lateral PFC on trustees' decisions, we applied rTMS to the right DLPFC or to the left DLPFC. The creation of a stimulation group receiving rTMS to the right DLPFC and a control group receiving rTMS to the left DLPFC was important to control for the potential side effects of rTMS (28), including discomfort, irritation, and mood changes. We also had another control condition in which we applied sham stimulation for 15 min to the right or left DLPFC. As mentioned earlier, we implemented an anonymous condition and a reputation condition. Thus, the experiment had a 2×3 design, with the factors ''condition'' (anonymous, reputation) and ''stimulation'' (left rTMS, right rTMS, sham) leading to 6 experimental groups. We randomly assigned each subject to 1 of the 6 groups.

Measurement of Fairness Norms. Because disruption of the PFC also might affect subjects' perception of what constitutes the social norm in a certain situation, we further elicited individuals' perception of fairness norms immediately after the trust game by confronting them with a hypothetical scenario. We asked participants to judge the fairness of a hypothetical trustee's behavior on a 7-point scale from ''very unfair'' to ''very fair.'' The scenario described an investor who invests 7 points while the trustee returns nothing.

Measurement of the Ability to Assess the Consequences of Past and Current Trustee Behaviors. Disruption of the PFC also might affect subjects' ability to assess the consequences of a particular reputation, that is, to assess the impact of actions on future social interaction—an abstract and cognitively demanding task. To rule out this explanation, we used another scenario to measure an

individual's assessment of the potential consequences of a certain reputation. We asked the subjects how many points (1, 4, 7, or 10) they would expect an investor to transfer to a trustee who had chosen to ''equalize payoff'' twice and to back-transfer nothing once.

Measurement of Dispositional Differences in Impulsivity and Reciprocity. Subjects completed personality questionnaires that assessed impulsivity (29), using the BIS and BAS scales, and personal norms of reciprocity (30). These questionnaires were completed roughly 10 days after the experiment.

Further details regarding our experimental protocol and analyses are provided in SI *Materials and Methods*. The instructions are available from the authors upon request.

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