Resisting the Power of Temptations

The Right Prefrontal Cortex and Self-Control

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ABSTRACT: Imagine you are overweight and you spot your favorite pastry in the storefront of a bakery. How do you manage to resist this temptation? Or to give other examples, how do you manage to restrain yourself from overspending or succumbing to sexual temptations? The present article summarizes two recent studies stressing the fundamental importance of inhibition in the process of decision making. Based on the results of these studies, we dare to claim that the capacity to resist temptation depends on the activity level of the right prefrontal cortex (PFC).

KEYWORDS: decision making; prefrontal cortex; self-control; transcranial magnetic stimulation; laterality

INTRODUCTION

The siren call of our impulses, desires, and urges often tempts us, and many of our decisions involve a conflict between our deliberate and our pleasure-seeking sides. From the standpoint of adaptive self-regulation, an appropriate response to temptations involves exercising self-control.[1–3] This conscious control of thought, action, and emotions may be considered as a distinctive feature of human cognition. Moreover, the ability to override immediate urges is not only relevant for adaptive *individual* decision making but also contributes to harmonious *social* interactions. For example, suppressing a desire to retaliate may be necessary to prevent the escalation of interpersonal conflict. Thus, our capacity to suppress the unlimited pursuit of immediate self-interest has been suggested to be a hallmark of civilized life.[4]

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A considerable amount of research has shown that the resistance to immediate self-interests is often greatly diminished in people with injuries to the prefrontal cortex (PFC).[5–7] This seems particularly true for patients with *right-sided* lesions.[8–10] However, patient studies are sometimes difficult to conduct due to limited opportunities for experimental manipulations. In addition, confounding variables, that is, the possibility of functional reorganization after brain lesions, may hamper the interpretation of the results, and studies often have a low number of patients (see Ref. 11 for limitations of the lesion method). Some functional imaging studies suggest that the *right* PFC may be particularly critical for self-regulation and self-control[12–15] or behavioral adjustments.[16] These studies, however, only passively measure brain activity correlated with a specific task, but do not reveal a causal relationship between changes in brain activity and their respective behavioral consequences. A direct investigation of such a causal brain–behavior relationship would require a controlled manipulation of brain activity where the impact on behavior or cognition can be quantified.[17] The technique of transcranial repetitive magnetic stimulation (TMS) allows for such a manipulation by inducing brief electric currents within discrete brain areas via pulsed magnetic fields on the corresponding scalp location. The "virtual lesion" technique in particular, that is, low-frequency repetitive transcranial magnetic stimulation (rTMS) over the course of several minutes, allows a transient disruption of cortical functions.[18] We applied this technique to examine whether self-control can be modified in healthy individuals in the context of both individual and social decision making.

Individual Decision Making: Diminished Self-Control Leads to Increased Risk-Taking Behavior

Adolescents generally exhibit riskier behavior than do adults. Their decision-making behavior is also thought to be a manifestation of an immature PFC,[19] and patients with traumatic brain injuries or other pathologies affecting the PFC show a tendency for riskier, "out-of-character" decision making, and an apparent disregard for negative consequences of their actions.[20,21] Clinical impressions tell us that this is particularly true for patients with right-sided lesions.[9,10] We designed a "virtual lesion" study[22] with healthy volunteers to investigate hemispheric asymmetries in risk-taking behavior directly. We used low-frequency rTMS to disrupt left or right dorsolateral prefrontal cortex (DLPFC) function transiently before applying a well-known gambling paradigm that provides a measure of risk taking ("risk task").[23] In this task, subjects have to decide between a relatively safe choice, which provides a low reward with a high probability, and a risky choice, which provides a substantially higher reward with a relatively low probability. Subjects were presented with binary choices between a safe and a risky choice. If subjects perceive the high reward to be salient, there may be a temptation to decide in favor of the risky choice. However, this choice has the drawback that the reward is only available with a low probability.

In the task, a series of six boxes on the screen indicated the probabilities of the different outcomes. The boxes can be either pink or blue, and the proportion of blue and pink boxes changed from one trial to another (5:1, 4:2, or 3:3; FIG. 1). The subject was told that the computer had arbitrarily hidden a "winning token" inside one of the blue or pink boxes. The subject had to decide whether the token was hidden in a box by pressing a button of the corresponding color.

Findings were straightforward. Participants stimulated over the right DLPFC ($N = 9$) were more likely to choose the high-risk prospect than those stimulated over the left DLPFC ($N = 9$) or those who received sham stimulation ($N = 9$) (FIG. 2A). We thus demonstrated that individuals display a significantly

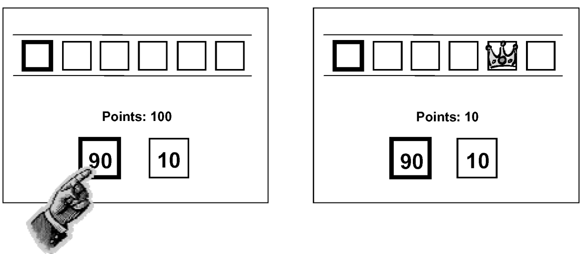

FIGURE 1. This figure shows one exemplary trial as displayed on the computer screen. Subjects were presented with six boxes colored pink or blue (in this black and white version of the figure pink boxes are replaced by white boxes with thick borders; blue boxes are replaced by boxes with thin borders). The number of pink and blue boxes varied from trial to trial according to a fixed pseudorandom sequence (sample shows "level of risk": 5:1). Subjects were asked to find the winning token. They did not have to pick the individual box hiding the winning token, but simply had to select the color of the box it was hidden in (illustrated in the left panel by a schematic hand pointing to the pink box in this example). Subjects were told that each box, regardless of color, was equally likely to hide the winning token. Thus, the likelihood of finding the winning token was directly related to the ratio of blue to pink boxes. For a trial showing 5 blue boxes and 1 pink box, there would be a probability of 5/6 that the winning token was hidden in a blue box, but only a 1/6 chance that it was hidden in the single pink box. Importantly, subjects are rewarded or penalized depending on whether they pick the correct color box or not. There is a fixed reward associated with either choice of boxes' color ("balance of reward": 10 vs. 90, 20 vs. 80, 30 vs. 70, and 40 vs. 60). The larger reward (and penalty) is always associated with choice of the high-risk prospect (i.e., the color with the fewer number of boxes), whereas the smallest reward (and penalty) is associated with choice of the low-risk prospect. A correct choice results in the addition of the number of points associated with that particular scenario, while an incorrect choice results in the subtraction of the same amount (sample in the right panel shows an incorrect choice that results in a subtraction of 90 points). Adapted from Knoch *et al.* 2006[22] (copyright 2006 by the Society for Neuroscience). This figure appears in color online.

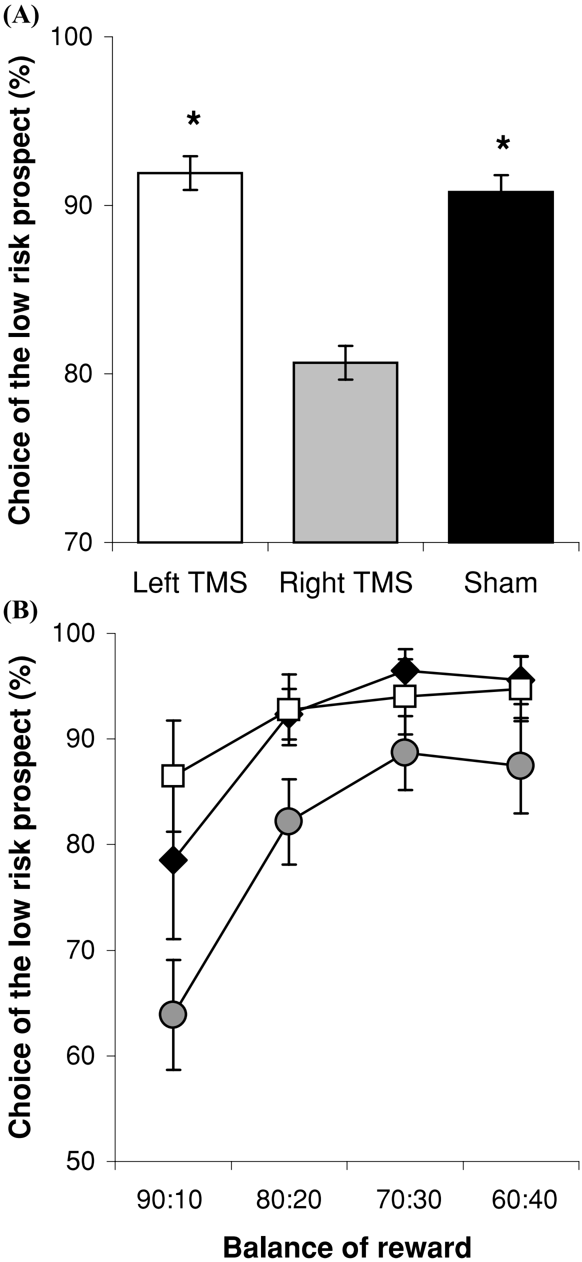

FIGURE 2. Percentage choice of the low-risk prospect (means ± SEM) (**A**) for all three groups, $P < 0.05$ and (**B**) as a function of the balance of reward (□ = Left TMS; ● = Right TMS; ♦ = Sham). Adapted from Knoch *et al.* [22] (copyright 2006 by the Society for Neuroscience).

stronger preference for the risky prospect, choosing the larger potential reward even at the risk of greater penalty, following disruption of the right, but not the left, DLPFC. We therefore suggest that the "risk task" primarily requires suppression of an option that appears seductive because of its large reward. That is, subjects are initially attracted to the high-reward/high-risk options by virtue of their higher payoffs, a tendency normally suppressed over the course of the task by top-down control mechanisms.

At this point we will discuss two alternative possible explanations of the rTMS effect, which are not considered in the original paper. For a discussion of additional alternative explanations, we ask the reader to refer to Ref. 22. The task requires subjects to measure the ratio of pink and blue boxes, and to take the various amounts of money associated with the different choices into account to calculate the expected value of the two options. Moreover, it requires subjects to integrate information about the rewarding and punishing consequences of an action. It may thus be that subjects receiving right prefrontal rTMS are impaired at calculating the riskiness of the choices or at integrating information about the choices' consequences. However, these interpretations are less convincing since repeated measures' analysis of variance (ANOVA) of group (left TMS, right TMS, sham) $\times$ level of risk (5:1, 4:2) $\times$ balance of reward (90:10, 80:20, 70:30, 60:40) revealed a main effect of balance of reward ($P < 0.001$) and, importantly, no interaction between group and balance of reward ($P = 0.414$; see FIG. 2B). In other words, if subjects were impaired in calculating or integrating the consequences of different choices, we should observe that subjects who received right rTMS are unable to discriminate between the different balances of reward. In addition, if subjects who received rTMS over the right PFC were impaired at calculating the riskiness of the choice, their deliberation time would probably be longer than that of subjects who received rTMS over left PFC or subjects who received sham stimulation. This was not the case. ANOVA of group $\times$ level of risk $\times$ balance of reward for the decision times revealed no main effect for group ($P = 0.737$). Therefore, we favor the hypothesis that the right PFC plays a crucial role in the suppression of superficially seductive options. We further speculate that the substantial differences among individuals in risk proneness in real-life scenarios may correspond to different levels of activity in the right PFC. The higher this level is, the lower one's "appetite for risk." If this turns out to be true, high-frequency rTMS (which increases cortical excitability) could be used to increase activity of the right PFC in a therapeutic framework to enhance cognitive control and adaptive decision making.

The results of this study led us to speculate whether increasing rather than decreasing the level of activity in the right PFC would diminish, rather than raise, subjects' "appetite for risk." Indeed, preliminary results show that participants with increased activity in the right DLPFC chose the safe prospect more often than did the sham group.[24]

Social Decision Making: Diminished Self-Control Leads to Selfish Behavior

The human species is unique to the extent that social norms that constrain the unrestricted pursuit of self-interest govern behavior. Overcoming the self's natural, impulsive nature requires self-control. The ultimatum game (UG) provides a useful tool for studying the neural mechanisms of self-control in the context of social decision making, as it illustrates the tension between economic self-interest on the one hand and fairness goals on the other. In this bargaining game, two anonymous individuals, a "proposer" and a "responder," have to agree on the division of a given amount of money, say \$10, according to the following rules: The proposer can make exactly one suggestion on how the \$10 should be allocated among the two by making an integer offer X to the responder. If the responder accepts, each player keeps the amount the proposer allocates. If the responder rejects the offer, neither player receives any money. If economic self-interest alone motivates the responder, he will accept even a very low offer, say \$1, because \$1 is better than \$0. However, if concerns for reciprocity[25] and equity[26] drive him, he may reject low offers, because he views them as insultingly unfair and inequitable. Thus, the responder faces a conflict in case of low offers between his economic self-interest, which drives him toward accepting the offer, and his fairness goals, which encourage him to reject it. Strong evidence[27,28] suggests that many people reject low offers in the game even if the stake level is as high as 3 months' income.[29] Rejection rates up to 80% have been observed[30] for offers below 25% of the available money, and a neuroimaging study[31] showed that both the anterior insula—a brain area involved in the evaluation and representation of negative emotional states[32]—and the DLPFC are activated when responders decide whether to accept or reject an unfair offer. For our purposes, it is particularly interesting that both the right and left DLPFC are more strongly activated when subjects face unfair offers compared to when they face fair offers. These areas are widely thought to be involved in executive control, goal maintenance, and the inhibition of prepotent responses.[33] All these functions are relevant for the responder in UG because there are likely to be several competing goals—fairness goals and self-interest—and the question is which of them should be maintained, that is, given priority, and which motivational impulse should be restrained.

The fact that the DLPFC is more strongly active when subjects are confronted with an unfair offer compared with a fair offer[31] cannot provide conclusive evidence that DLPFC activity is crucial for the responders' decisions. In principle, it is even possible that this area is not causally involved in the decision to accept or reject unfair offers. To address this question, we applied prefrontal low-frequency rTMS to 52 subjects[34] (left DLPFC, $N = 17$; right DLPFC, $N = 19$; sham, $N = 16$) who were in the role of the responder in an anonymous UG with a stake size of CHF 20 (CHF 1 $\approx$ \$ 0.80). To generate enough observations on the responders' side, we limited the proposer's strategy space, meaning that only offers of CHF 10, 8, 6, or 4 were possible. Obviously, CHF 10 is the fairest offer, because it splits the stake size equally, while CHF 4 is the most unfair offer.

If the DLPFC is involved in overriding selfish impulses that drive a subject toward acceptance of unfair offers, low-frequency rTMS of this brain region should *increase* the acceptance rate for unfair offers relative to the sham stimulation condition, as this kind of stimulation leads to a disruption of neuronal firing in the stimulated brain region.[18] In other words, if we disrupt activity in a brain region that is hypothesized to override selfish impulses, we should functionally weaken the inhibitory control and, selfish impulses should thus have a stronger impact on decision making; as a consequence, the acceptance rate of unfair offers should increase. We focus on acceptance behavior with regard to the lowest offer in this case because the tension between fairness and self-interest is greatest here. FIGURE 3A indicates that the right DLPFC group has a significantly higher acceptance rate than the left DLPFC and the sham rTMS group. Importantly, these differences across conditions cannot be attributed to different fairness judgments across groups. Immediately after the ultimatum game experiment, we elicited subjects' fairness judgments with regard to different offers on a 7-point scale. Subjects in all three treatment groups judged the lowest offer of 4 as rather unfair and there are no differences in fairness judgments across groups (FIG. 3B). Thus, despite the fact that subjects in all three groups judge low offers as very unfair, subjects whose right DLPFC has been disrupted exhibit much higher acceptance rates. Similar results were found for the other unfair offer of 6 CHF.

These results suggest that subjects who received right prefrontal TMS are less able to resist the economic temptation to accept unfair offers. Our findings are also interesting in the light of evidence suggesting that patients with right prefrontal lesions are characterized by the inability to behave in normatively appropriate ways despite the fact that they possess the social knowledge that is necessary for normative behavior.[35]Our findings are also congruent with the observation of empathy deficits in patients with predominantly right frontal lesions,[36,37] as an inhibitory component is required to regulate and tone down the prepotent self-perspective to allow the perception and evaluation of others' perspectives.[38] Further support comes from findings in patients with frontotemporal dementia (FTD), showing that symptoms may be influenced by the relative involvement of the right versus the left hemisphere, with left-sided FTD manifesting language changes and right-sided FTD presenting with aggressive, antisocial, and other socially undesirable behaviors.[39]

Note that if we suggest that right DLPFC is involved in overriding self-interest motives, we do not necessarily imply that this brain region directly suppresses other brain areas that represent self-interest. Instead, we believe that right DLPFC is involved in top-down control (or executive control), the overall effect of which is a reduction in the weight of self-interested impulses on an individual's action. Thus, rather than directly suppressing neural activities that

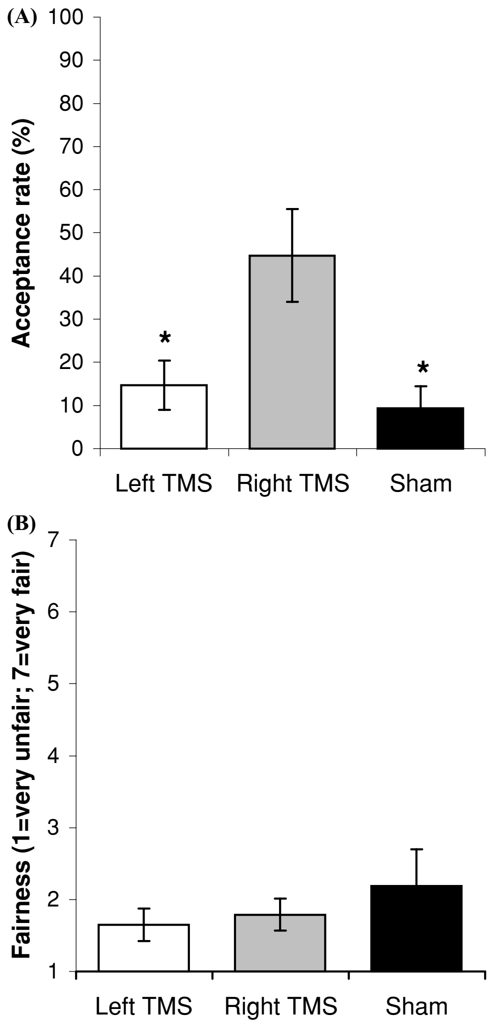

FIGURE 3. Behavioral responses and fairness judgments (means ± SEM) related to the most unfair offer of CHF 4. (**A**) Acceptance rates across treatment groups. Subjects whose right DLPFC is disrupted exhibit a much higher acceptance rate than subjects in the other two treatments (Mann–Whitney U tests, two-tailed, $P < 0.05$). (**B**) Perceived unfairness across treatments (1 = very unfair; 7 = very fair). Subjects in all three treatment groups perceive an offer of 4 as very unfair, and there are no significant differences across groups. Responders were shown a list of all feasible offers in the human- and the computer-offer condition and asked to report on a 7-point scale to what extent they perceived an offer as fair or unfair (1 = very unfair; 7 = very fair). As the ultimatum game experiment lasted only a short time, these fairness assessments took place roughly 4–5 min after the 15-min offline stimulation with rTMS. Thus, when subjects assessed the fairness of different offers, their DLPFC was still disrupted if they had received real rTMS stimulation. Adapted from Knoch *et al.*[34].

represent self-interested impulses, the DLPFC may be part of a network that modulates the relative impact of fairness motives and self-interest goals on decision making, and the final outcome of this modulation may then be a weakening of the impact of self-interest motives on decision making.

Evidence from human lesion studies has implicated the right hemisphere in the processing of emotional and social information.[40,41] Can a reduced general emotional responsiveness explain the observed rTMS effect after right prefrontal rTMS stimulation? This seems to be unlikely for the following reasons: rTMS of the right DLPFC reduces fair behaviors but not fairness judgments. As there is no reason to believe that emotions are less involved in fairness judgments than in fair behaviors, a general reduction in emotional responsiveness should have also affected fairness judgments. Moreover, we had an additional treatment condition that we did not yet mention in this article. In our experiment, a responder not only played the usual ultimatum game for 10 rounds where the human partner proposes a division of the available money (human-offer condition), but every subject also played 10 rounds with human partners who could not make proposals themselves. A computer randomly generated the offers in these trials (computer-offer condition). The motive to punish the human partner for an unfair offer cannot play a role in the computer-offer condition, because the partner is not responsible for it. According to the theory of inequity aversion,[26] many subjects find accepting low offers per se aversive, even if made by a computer. Indeed, a considerable share (33%) of low offers was rejected in the computer-offer condition. A general reduction in emotional responsiveness by rTMS of the right DLPFC also should have affected behavior in the computer-offer condition significantly because there is no reason to believe that an aversion against inequality is associated with less emotional involvement. We could not find such an effect, however; low-frequency rTMS of the right DLPFC did not increase the acceptance rate in the computer-offer condition ($P = 0.306$). Finally, if rTMS simply reduces subjects' emotional responsiveness, we should also expect an impact on subjects' mood. We measured mood before and after rTMS using visual analogue scales and could not find any effect of rTMS on mood (see FIG. 4). We therefore favor the hypothesis that the right DLPFC is causally involved in a neural network that controls or regulates the impact of the economic temptation on the acceptance decision. This interpretation can explain why rTMS affects fair behavior but not fairness judgments because no economic temptation is involved in fairness *judgments,* whereas the rejection of an unfair but positive offer requires foregoing economic gains.

As the right frontal lobe seems to be relevant for the integration of information[42,43] one might be tempted to suggest alternatively that right prefrontal rTMS causes an impairment in the ability to integrate different decision values—the positive monetary value of the gain and the negative value of unfairness. This hypothesis, however, cannot easily account for the fact that we observed treatment differences regarding the response times in accepting

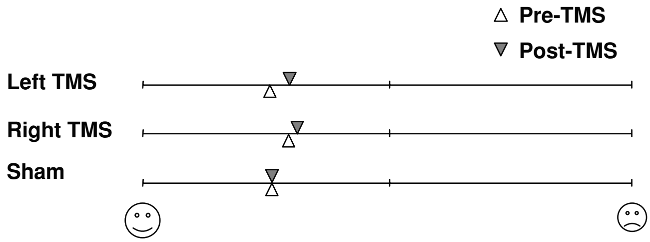

FIGURE 4. Subjects' moods as indicated on a visual analogue scale. Subjects' moods are predominantly positive in all treatments. Neither before the application of rTMS (Kruskall–Wallis Test, $P = 0.659$) nor after the application (Kruskall–Wallis Test, $P = 0.773$) did we observe mood differences across treatments. There are also no treatment differences in the change in mood (Kruskall–Wallis Test, $P = 0.970$).

unfair offers, while there are no differences in response times when subjects face a fair offer. If integrating different decision values is more difficult after right rTMS of the DLPFC, subjects should exhibit longer response times in all situations. However, rTMS of the right DLPFC did not affect response times when subjects faced fair offers, and the response time *decreases* strongly for subjects whose right PFC was disrupted when they faced unfair offers of 4 in the human-offer condition.

In conclusion, the findings in these studies suggest that cortical stimulation can modulate the fundamental human capacity of self-control, and the results thus confirm the asymmetric role of the PFC in decision making. They also indicate that the capacity for restraint depends on the activity level of the right PFC. In response override, one must stop a prepotent response to a stimulus, either because the response needs to be withheld or because a less prepotent response is more appropriate. Without this capacity, we would be slaves of our emotional impulses, temptations, and desires and thus unable to behave socially adequately. Our findings also illustrate the importance of rTMS for further progress in understanding the neural basis of decision making. Although neuroimaging data indicate that responders' left DLPFC is activated when they face unfair offers,[32] disruption of the left DLPFC does not change their behavior, suggesting that neuroimaging studies need to be complemented with techniques, such as rTMS, to reach more firm conclusions. Since our data suggest that the right lateral PFC is causally involved in overriding self-interest, it would be interesting to investigate whether decreasing the activity level of right PFC results in immoral decision making, as moral decisions often require the inhibition of self-interest.

Even though the application of TMS enables us to claim a causal role of lateral PFC activity for self-control processes in the context of individual and social decision making, the exact neuronal mechanisms underlying the TMS-induced virtual lesion will remain unknown until a simultaneous examination of underlying brain activity during task performance can be performed. Therefore, the combination of TMS-induced virtual lesions and fMRI during a given task promises important additional insights for studying the neural mechanisms of self-control.

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