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Figs. S1 and S2

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Self-Control in Decision-Making Involves Modulation of the vmPFC Valuation System

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Every day, individuals make dozens of choices between an alternative with higher overall value and a more tempting but ultimately inferior option. Optimal decision-making requires self-control. We propose two hypotheses about the neurobiology of self-control: (i) Goal-directed decisions have their basis in a common value signal encoded in ventromedial prefrontal cortex (vmPFC), and (ii) exercising self-control involves the modulation of this value signal by dorsolateral prefrontal cortex (DLPFC). We used functional magnetic resonance imaging to monitor brain activity while dieters engaged in real decisions about food consumption. Activity in vmPFC was correlated with goal values regardless of the amount of self-control. It incorporated both taste and health in self-controllers but only taste in non–self-controllers. Activity in DLPFC increased when subjects exercised self-control and correlated with activity in vmPFC.

The concept of self-control in decision-making has occupied philosophers and scientists throughout recorded history because the ability to exercise it is central to human success and well-being. Behavioral studies have examined the problem of self-control and provided valuable insights that suggest it is exhaustible in the short term (*1*–*3*), can be enhanced by cognitive strategies (*4*–*7*), and is correlated with measures of intelligence (*8*–*10*). However, little is known about the neurobiological underpinnings of self-control and how these neural mechanisms might differ between successful and unsuccessful self-controllers.

We investigated which neural processes are responsible for the deployment of self-control and how these processes interact with the brain's valuation and decision-making circuitry. We hypothesized that goal-directed decisions have their basis in a value signal encoded in the ventromedial prefrontal cortex (vmPFC). This hypothesis has its basis in neuroimaging studies that have found a correlation between activity in this area and behavioral measures of value (*11*–*16*), as well as findings from electrophysiology studies (*17*, *18*). We also hypothesized that self-control involves modulation by the dorsolateral prefrontal cortex (DLPFC) of the value signals computed in vmPFC. This hypothesis has its basis in the role of DLPFC in cognitive control (*19*, *20*), working memory (*21*, *22*), and emotion regulation (*23*).

To test these hypotheses, we recruited self-reported dieters and used functional magnetic resonance imaging (fMRI) to study the neural activity in vmPFC and DLPFC while the participants made real decisions about which foods to eat. Participants performed three tasks in the scanner (Fig. 1A) (*24*). In the first two parts, they rated 50 different food items for taste and health separately. On the basis of these ratings, we selected a reference item for each subject that was rated neutral in both taste and health. In the final part, subjects were asked to choose between each of the foods and the reference item. One decision was randomly selected and implemented at the end of the study. Participants indicated the strength of their decision by using a five-point scale (strong no, no, neutral, yes, and strong yes), which provided a measure of their relative value for eating that food instead of the reference item. Following the previous literature (*11*), we refer to this measure as a goal value, which refers to the amount of expected reward associated with consuming the food. Note that dieters should be concerned with the healthiness of the foods, and not only with their taste, and that optimal decision-making requires integrating these two separate concerns.

Participants were classified as self-controllers (SCs; $n = 19$) or non–self-controllers (NSCs; $n = 18$) on the basis of their decisions (*24*). There was a stark difference between the SC and NSC groups (Fig. 1B): Whereas SCs made decisions on the basis of both health and taste, rejecting most liked-but-unhealthy items, the NSC group made decisions on the basis of taste alone.

We made four predictions about the patterns of neural activity, which we tested by using the fMRI data. First, activity in vmPFC should be correlated with participants' goal values regardless of whether or not they exercise self-control. Second, activity in the vmPFC should reflect the health ratings in the SC group but not in the NSC group. Third, the DLPFC should be more active during successful than failed self-control trials. Fourth, DLPFC and vmPFC should exhibit functional connectivity during self-control trials.

We tested the first prediction by estimating a general linear model (GLM) of blood oxygen

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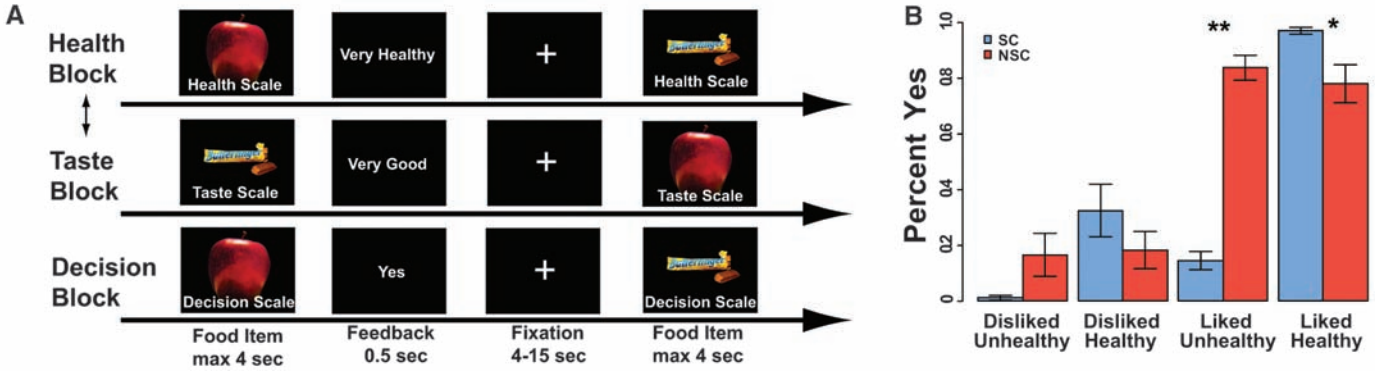

Fig. 1. (**A**) The task proceeded in three parts: taste ratings, health ratings, and decisions. (**B**) Percentage of the time participants chose the food over the reference item. The SC group chose not to eat liked-unhealthy food items more often than the NSC group did (**$t_{31} = 12.5$; $P < 0.0000$). The SC group also ate liked-healthy food items more often than the NSC group did (*$t_{18} = 2.74$; $P < 0.05$). Error bars denote standard errors.

level–dependent activity that included a parametric regressor for goal values at the time of evaluation. Activity in vmPFC was correlated with goal values for all participants regardless of the amount of self-control exercised (Fig. 2, A and B; fig. S1; and table S2). The areas of vmPFC identified largely overlap with regions that have been associated with valuation in other tasks that require no self-control (*11*–*15*) (Fig. 2C).

To test the second prediction, we estimated a new GLM that included parametric regressors for health and taste ratings. The beta values for both parametric regressors were extracted from the voxels in vmPFC that exhibited the strongest correlation with goal values for each participant. In the SC group, vmPFC activity was modulated by both health (t_{18} = 4.20, P < 0.001) and taste (t_{18} = 3.31, P < 0.005) (Fig. 2D), whereas in the NSC group it was only modulated by taste (t_{17} = 7.28, P < 0.001). We tested this relationship further by estimating a linear regression of the impact of health ratings on each participant's behavior against a measure of the impact of health ratings on the participant's vmPFC activity (regression coefficient = 0.847, t_{35} = 5.57, P < 0.001) (Fig. 2E).

We tested the third prediction by comparing the neural responses during the decision period in three different types of trials: those in which self-control was not needed, those in which self-control was successfully deployed, and those in which participants failed to use self-control. We found greater left DLPFC activity [inferior frontal gyrus (IFG) and Brodmann's area (BA) 9 (IGF/BA9)] in the SC group than in the NSC group during successful self-control trials (Fig. 3A and table S3). However, both groups had greater activity in this region for successful self-control trials compared with that of failed self-control trials (SC group t_{14} = 2.29, NSC group t_{13} = 2.62, P < 0.05) (Fig. 3B).

We tested the fourth prediction by performing a linear regression of left DLPFC activity during self-control trials on the response of vmPFC to the presentation of liked-but-unhealthy food items (regression coefficient = –0.688, t_{17} = –2.26; P < 0.05) (Fig. 3C). Self-control in this type of trial requires ramping down the weight given to taste in computing the goal value. A similar decrease in vmPFC activity was seen in gamblers who chose not to gamble in losing conditions (*25*).

We also investigated whether left DLPFC and vmPFC exhibited task-related functional connectivity. An initial analysis of the psychophysiological interactions (PPI) using left DLPFC as the seed showed connectivity with several regions (fig. S4 and table S4), including the left IFG/BA46 but not the vmPFC, which ruled out direct modulation from DLPFC. However, DLPFC might modulate the vmPFC through its effect in a third region, such as IFG/BA46. This area was of particular interest because it is involved in working memory and goal maintenance (*21*, *22*), it has anatomical connections to vmPFC (*26*), and previous studies have shown that IFG/BA46 activity is correlated with goal values (*11*, *13*). Thus, we used this area as the seed for a second PPI analysis and found positive task-related functional connectivity with the vmPFC (fig. S3 and table S5). A conjunction analysis confirmed that this was the same area of vmPFC that was correlated with goal values. Thus, the vmPFC was functionally connected to the left DLPFC through a two-node network (Fig. 4, B and C).

The results provide insight into two open questions in behavioral neuroscience. First, they suggest that self-control problems arise in situations where various factors (e.g., health and taste) must be integrated in vmPFC to compute goal values and that DLPFC activity is required for higher-order factors, such as health, to be incorporated into the vmPFC value signal. We speculate that the vmPFC originally evolved to forecast the short-term value of stimuli and that humans developed the ability to incorporate long-term considerations into values by giving structures such as the DLPFC the ability to modulate the basic value signal.

Second, a fundamental difference between successful and failed self-control might be the extent to which the DLPFC can modulate the vmPFC. Individual differences in the ability of DLPFC to modulate vmPFC might be due to differences within the DLPFC or to differences in connectivity between the DLPFC and other areas. The areas of DLPFC that we have found to play a role in self-control are similar to areas that are at work in cognitive control (*27*, *28*) and in emotional regulation (*23*, *29*). Our results are consistent with previous theories of the role of DLPFC in cognitive control, which posit that it sends signals to other brain regions to promote task-relevant processing and suppress irrelevant activity (*20*). Thus, our findings could be the start of an explanation for why general intelligence, cognitive control, and emotional regulation are all correlated with various behavioral measures of self-control (*5*, *8*–*10*).

Our findings also have implications for an ongoing debate in decision neuroscience and psychology. McClure *et al*. (*30*, *31*) have proposed that intertemporal choice involves the interaction of multiple independent valuation systems (some characterized by very large discount rates and a hypersensitivity to immediate rewards and others that are more patient and thus more sensitive to long-term considerations) that compete with each other for behavioral control. They have also proposed that the shortsighted valuation network includes the vmPFC and that the foresighted one includes the DLPFC. In contrast, Kable and Glimcher (*12*) have argued that there is a common valuation system and that the values that guide behavior are computed in the vmPFC-striatal network. However, they do not provide any theory or evidence about which neural mechanisms

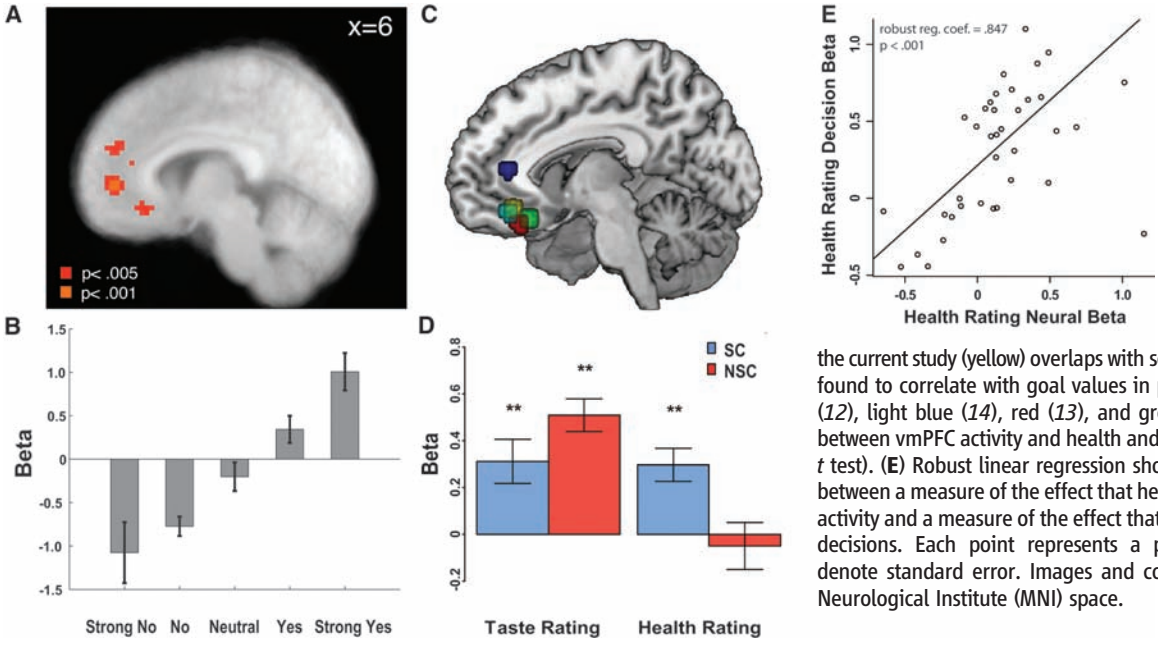

Fig. 2. (**A**) Regions of vmPFC in which activity correlated with goal values across all participants and regardless of their degree of self-control. See tables S1 to S5 for the statistics corrected for multiple comparisons. (**B**) Beta values in vmPFC increased with goal values. (**C**) The vmPFC area reflecting goal values in the current study (yellow) overlaps with several areas that have been found to correlate with goal values in previous studies [dark blue (*12*), light blue (*14*), red (*13*), and green (*11*)]. (**D**) Correlations between vmPFC activity and health and taste ratings (**P < 0.005, t test). (**E**) Robust linear regression showing a strong relationship between a measure of the effect that health ratings have on vmPFC activity and a measure of the effect that the health ratings have on decisions. Each point represents a participant. All error bars denote standard error. Images and coordinates are in Montreal Neurological Institute (MNI) space.

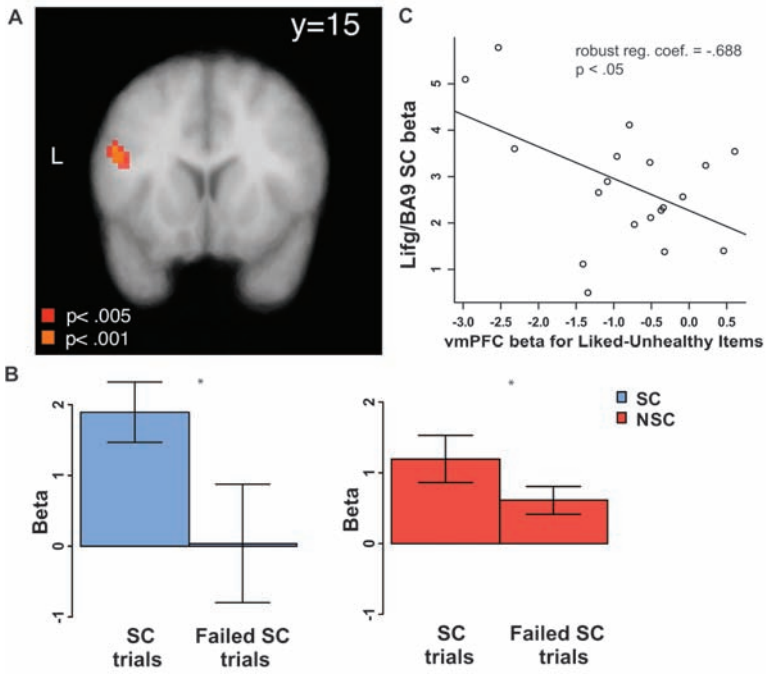

Fig. 3. (**A**) Region of left DLPFC showing greater activity in successful self-control trials in the SC than the NSC group. Images and coordinates are in MNI space. (**B**) Both groups showed greater activity in DLPFC for successful versus failed self-control trials (*$P < 0.05$, paired t test). (**C**) Activity in left DLPFC (IFG/BA9) was negatively correlated with vmPFC activity in the SC group during trials in which liked-but-unhealthy foods were avoided. Each point represents a participant in the SC group.

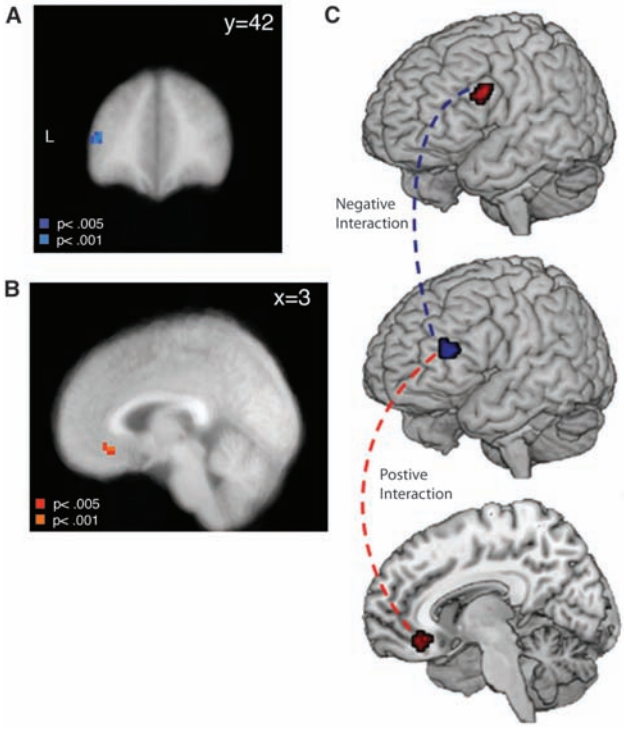

Fig. 4. (**A**) Left IFG/BA46 showed negative task-related functional connectivity with the left DLPFC during decisions about unhealthy items by the SC group. (**B**) Conjunction analysis showing voxels that were correlated with goal values and exhibiting significant positive task-related functional connectivity with IFG/BA46 (reported P values based on the PPI analysis). (**C**) Diagram summarizing the results of the PPI analyses and illustrating the path through which the left DLPFC might modulate activity in the vmPFC. Blue lines represent negative interactions, and red lines represent positive ones. Images and coordinates are in MNI space.

modulate the value signal in order to exercise self-control. Our results bring a substantial amount of resolution to this debate. Like Kable and Glimcher, we find strong evidence for the existence of a common valuation signal in the vmPFC that drives choices regardless of the degree of self-control deployed by the participants. Like McClure *et al*., our results suggest that the DLPFC plays a critical role in the deployment of self-control. Contrary to their theory, however, we show that this is not because an alternative value signal is encoded in DLPFC, which in our experiment would require a nonexistent correlation between activity in this area and the health ratings (fig. S5). Instead, the DLPFC influences self-control by modulating the value signal encoded in vmPFC.

Lastly, an improved understanding of the neurobiology of self-control in decision-making will have applications to clinical practice in domains such as obesity and addiction, to economic and public policy analysis in problems such as suboptimal savings and health behaviors, and to legal thinking about which criteria should be used in determining if an individual is in full command of his decision-making faculties and thus accountable to the law.

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