

Self-Regulatory Depletion Enhances Neural Responses to Rewards and Impairs Top-Down Control

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Abstract

To be successful at self-regulation, individuals must be able to resist impulses and desires. The strength model of self-regulation suggests that when self-regulatory capacity is depleted, self-control deficits result from a failure to engage top-down control mechanisms. Using functional neuroimaging, we examined changes in brain activity in response to viewing desirable foods among 31 chronic dieters, half of whom completed a task known to result in self-regulatory depletion. Compared with nondepleted dieters, depleted dieters exhibited greater food-cue-related activity in the orbitofrontal cortex, a brain area associated with coding the reward value and liking aspects of desirable foods; they also showed decreased functional connectivity between this area and the inferior frontal gyrus, a region commonly implicated in self-control. These findings suggest that self-regulatory depletion provokes self-control failure by reducing connectivity between brain regions that are involved in cognitive control and those that represent rewards, thereby decreasing the capacity to resist temptations.

Keywords

self-regulation, self-control, depletion, reward, food, orbitofrontal cortex, fMRI

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Failures of self-control are responsible for a wide variety of societal ills. Difficulty inhibiting urges and regulating desires lie at the root of such current health concerns as obesity and substance abuse. Contemporary models of self-regulation, such as the strength model of self-control (Baumeister & Heatherton, 1996), emphasize the role of a limited-capacity resource that, when exhausted, increases the enactment of unwanted behaviors. For example, self-regulatory resource depletion leads dieters to break their diets and overeat (Hofmann, Rauch, & Gawronski, 2007; Vohs & Heatherton, 2000), smokers to smoke (Shmueli & Prochaska, 2009), and social drinkers to drink more (Muraven, Collins, & Nienhaus, 2002). Since it was first formulated, the strength model has been supported by a wide array of studies both inside the laboratory (for a meta-analysis, see Hagger, Wood, Stiff, & Chatzisarantis, 2010) and outside the laboratory (e.g., Hofmann, Vohs, & Baumeister, 2012). Despite the wealth of evidence supporting this model of self-control, the precise mechanism by which successive acts

of self-regulation can engender self-regulatory collapse is widely debated (Beedie & Lane, 2011; Inzlicht & Schmeichel, 2012; Job, Dweck, & Walton, 2010; Kurzban, 2010; Schmeichel, Harmon-Jones, & Harmon-Jones, 2010).

Recently, a number of researchers have argued that current formulations of the strength model may overemphasize the role of weakened restraint and impaired control in self-regulation failures. For instance, Schmeichel et al. (2010) noted that prior work showing increased consumption of pleasurable foods after depletion can be interpreted as evidence of weakened control, increased impulse strength, or a combination of both. Indeed, they found that self-regulatory depletion improves, rather than interferes with, the ability to detect rewarding stimuli.

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Likewise, Vohs et al. (2012) demonstrated that self-regulatory depletion increases the strength of desires and emotions in the absence of any demands to regulate behavior. For example, they showed that following depletion, participants rated pleasant images more favorably, found pain more intense, and, upon exposure to appetizing food, reported greater desires to consume the food. Together, these new findings suggest that self-regulatory depletion may act directly on the strength of desires, increasing the lure and pull of temptations and thereby rendering them more difficult to resist.

How might self-regulatory depletion lead to an intensification of desires? One recent theory proposes that depletion interferes with the ability to monitor the environment for situations and cues that conflict with goals, which in turn increases the likelihood of attending and responding to rewarding stimuli (Inzlicht & Schmeichel, 2012). In other words, people often desire rewarding items and experiences (e.g., food, sex, or Facebook) but spend a considerable portion of their waking hours keeping these desires in check (see Hofmann et al., 2012). When the capacity to self-regulate is depleted, self-monitoring is reduced, and motivation shifts toward gratification.

Another mechanism, one that is not incompatible with this theory, comes from a recent neural-systems model of self-regulation failure proposed by Heatherton and Wagner (2011). In this *balance* model of self-regulation, ongoing self-control is sustained by a balance between brain regions involved in impulse control (i.e., lateral and medial regions of the prefrontal cortex) and brain areas involved in representing the reward value, desirability, and emotional valence of stimuli (e.g., the orbitofrontal cortex, or OFC, and striatum). According to this model, self-control fails when the strength of an impulse exceeds the capacity to regulate it, such as might occur during adolescence when frontal control is still developing (Somerville, Jones, & Casey, 2010). The model also suggests that impulse strength is under constant moderation from regions involved in top-down control; therefore, any disruption of executive control can lead to increased impulse strength. According to this model, then, depletion operates by disrupting frontal control, thereby releasing brain regions involved in representing the reward value of temptations.

In the current study, we used functional neuroimaging in conjunction with a well-validated food-cue reactivity task (i.e., Demos, Heatherton, & Kelley, 2012; Demos, Kelley, & Heatherton, 2011; Wagner, Boswell, Kelley, & Heatherton, 2012) to examine two questions about how self-regulatory depletion disrupts brain mechanisms involved in self-control: (a) Does self-regulatory depletion increase the reward value of a naturally rewarding stimulus, such as high-calorie appetizing food? (b) Does self-regulatory depletion interfere with top-down control mechanisms that serve to inhibit desires for appetizing

foods in a population that is strongly motivated to control their eating (i.e., chronic dieters)? Food was an ideal stimulus to use because it is a natural reward that is both required and desired by animals and humans alike, and because there are people (chronic dieters) who are highly motivated to limit their consumption of it (e.g., Heatherton, Polivy, & Herman, 1991).

We predicted that, compared with a group of nondepleted dieters, those who underwent self-regulatory depletion would show increased food-cue-related activity in brain regions associated with the subjective reward value of food (i.e., OFC, ventral striatum; Beaver et al., 2006; Demos et al., 2012; Demos et al., 2011; Gottfried, O'Doherty, & Dolan, 2003; Kringelbach, O'Doherty, Rolls, & Andrews, 2003; Wagner et al., 2012; for a meta-analysis, see Van der Laan, De Ridder, Viergever, & Smeets, 2011). In addition, we predicted that depleted dieters would show impaired recruitment of lateral prefrontal regions (i.e., the inferior frontal gyrus, or IFG) involved in cognitive control and self-regulation (Berkman, Falk, & Lieberman, 2011; Hare, Camerer, & Rangel, 2009; Kober et al., 2010; Somerville, Hare, & Casey, 2011).

Method

Participants

Thirty-three healthy, right-handed female chronic dieters were recruited from a larger pool of participants who completed the Revised Restraint Scale (Heatherton, Herman, Polivy, King, & McGree, 1988), a validated measure of chronic dieting tendencies. Participants with restraint scores greater than 16 were considered to be chronic dieters (see Heatherton et al., 1991) and were invited to participate in the study. Dieting was not mentioned during recruitment, and participants remained unaware of our selection criteria until debriefing. Participants were randomly assigned to the depleted or the control group. Two participants were excluded from analysis because of excessive movement during scanning (i.e., several incidences of movement greater than 2 mm), which left a total of 31 participants (16 in the depleted group, 15 in the control group). Reaction time data for 2 participants were lost because of equipment malfunction. There were no differences between participants in the depleted and control groups with respect to demographic and dieting characteristics (Table 1). All participants gave informed consent in accordance with the guidelines set by the Committee for the Protection of Human Subjects at Dartmouth College.

Procedure

Participants were instructed to refrain from eating or drinking for at least 2 hr prior to the experimental

Table 1. Characteristics of Dieters in the Depletion and Control Groups

Measure	Depleted group ($n = 16$)	Control group ($n = 15$)
Age (years)	19.3	18.9
Weight (pounds)	128.3	127.5
Estimated BMI (kg/m^2)	20.7	20.6
Hours slept the previous night	7.4	7.8
Hours since last meal	7.4	5.7
Current hunger (1 to 5)	2.6	2.7
Restraint Scale Score	19.2	18.1

Note: There were no between-group differences in age, weight, estimated body mass index (BMI), hours slept, hours since the last meal, current hunger, or restraint scores (all $ps > .25$). Restraint was measured with the Revised Restraint Scale (Heatherton, Herman, Polivy, King, & McGree, 1988). Current hunger was rated on a scale from 1, *not at all hungry*, to 5, *extremely hungry*.

session, so that they did not arrive satiated. They were informed that they would be participating in two unrelated experiments: understanding the gist of a movie and categorizing scenes (for an overview of the experimental procedure and stimuli, see Fig. S1 in the Supplemental Material).

Attention-control task. Participants first performed an attention-control task, which was adapted from a task that is commonly used in studies of self-regulatory resource depletion (e.g., Schmeichel, Vohs, & Baumeister, 2003). For this task, participants viewed 7 min of a documentary on Canadian bighorn mountain sheep (Brind & Schmalz, 1970). During the video, a series of one- and two-syllable distractor words (total of 40 words) appeared at the bottom of the screen and moved to the center over the course of 3 s. Participants in both groups were instructed to keep their gaze on the video at all times. Those in the control group were told that they could freely read the words, whereas those in the depleted group were instructed to inhibit reading while maintaining attention on the video. Participants in the depleted group were not expected to successfully avoid reading all the distractor words; rather, the purpose of the task was to have them exert self-regulatory effort over an extended period of time.

This task was preceded by a bogus eye-tracking calibration session designed to convince participants that their gaze was being monitored during scanning. In order to maintain our cover story, we had participants undergo scanning during the attention-control task. We note, however, that the task was not designed to be amenable to functional MRI (fMRI) analysis, and scanning was done purely to ensure that participants believed the task to be relevant to the overall experiment and thus remained motivated. (For more details on the task, see Wagner & Heatherton, 2012; for more details on the bogus eye-tracking calibration, see Supplementary Methods in the Supplemental Material available online.)

Food-cue reactivity task. After completing the attention-control task, participants underwent fMRI scanning while performing a food-cue reactivity task, which was modified from a task used in our prior research on neural cue reactivity to appetizing foods (Demos et al., 2011; Wagner et al., 2012). To minimize the delay between the self-regulatory depletion (attention-control task) and the food-cue reactivity task, we provided instructions for the latter prior to the start of the experiment.

Appetizing food stimuli for this task were selected on the basis of a pilot test in which 25 participants rated 250 high-quality food images according to how much they liked and craved the depicted food items. The final set of food images consisted of the 30 most liked and craved foods from each of three categories (meals, snacks, and desserts). One hundred eighty images involving people or natural scenes, such as landscapes, were chosen to be used in a control condition. This task used a rapid event-related design with image trials consisting of a single image (food, people, or nature image) displayed for 2,000 ms. In addition, null-event trials consisting of a white fixation cross against a black background were used to introduce jitter into the fMRI time series in order to increase the efficiency of estimating task effects. The order of trial types and the duration of the intertrial interval (500 ms, 3,000 ms, or 5,500 ms) were pseudorandomized. On image trials, subjects indicated via a button press whether the image showed an indoor or outdoor scene. This incidental task ensured that participants remained alert and naive to the purpose of the study.

Final measures and debriefing. After fMRI scanning, participants rated how much they liked each of the food items in the images (on a scale from 1 to 9). They also completed a questionnaire probing for suspicion and rated the depletion task in terms of difficulty and cognitive fatigue (on scales from 1 to 7). These ratings were combined to create a self-report index of the subjective experience of depletion. In addition, participants

answered questions regarding their current hunger level, the amount of hours they had slept the previous evening, and the number of hours that had passed since their last meal.

Image preprocessing and analysis

Participants were scanned on a Philips Achieve 3.0-T scanner (for additional image acquisition details, see Supplementary Methods in the Supplemental Material). The fMRI data for the food-cue reactivity task were analyzed using the general linear model (GLM) for event-related designs in SPM8 (Wellcome Department of Cognitive Neurology, London, England) in conjunction with a suite of tools for preprocessing and analysis (available at <http://github.com/ddwagner/SPM8w>). For each functional run, data were preprocessed to remove sources of noise and artifact. Images were corrected for differences in acquisition time between slices, realigned within and across runs, and unwarped to reduce residual movement-related image distortions. Data were normalized into a standard stereotaxic space (3-mm isotropic voxels) based on the SPM8 EPI template, which conforms to the International Consortium for Brain Mapping 152 brain template space. Normalized images were spatially smoothed with a 6-mm full-width-at-half-maximum Gaussian kernel.

For each participant, a GLM incorporating task effects and covariates of no interest (a session mean, a linear trend to account for low-frequency drift, and six movement parameters) was constructed and convolved with a canonical hemodynamic response function (HRF). Additional nuisance regressors were included for 2 participants who exhibited a small number of isolated movements of more than 2 mm (one regressor per affected volume and two additional regressors for the volume preceding and following the movement). In addition, we conducted a parametric modulation analysis in which participants' idiosyncratic liking ratings for each food image were used as a parametric modulator of the height of the hemodynamic response during food trials.

Next, contrast images comparing food and control trials were created for each subject and entered into a second-level, random-effects analysis. Monte Carlo simulations using AlphaSim (Ward, 2000) were used to calculate the minimum cluster size at an uncorrected threshold of $p < .001$, required for a whole-brain correction of $p < .05$. Simulations (10,000 iterations) were performed using the mean across-subject smoothness estimated from the residuals obtained from each participant's first-level GLM. These simulations indicated that a minimum cluster size of 33 contiguous voxels was required for whole-brain correction. Given our strong a priori predictions regarding the role of the ventral striatum in food-cue

reactivity, we applied a small-volume correction using an anatomical mask of the nucleus accumbens, defined using the labels provided with the Harvard-Oxford probabilistic atlas of cortical and subcortical structures (Desikan et al., 2006). This resulted in a small-volume correction of 9 contiguous voxels (cluster-defining threshold of $p < .005$) for a correction of $p < .05$ within the volume of the nucleus accumbens.

Subsequent between-group comparisons were conducted using region-of-interest (ROI) analyses. For each ROI, the parameter estimate was extracted using a spherical ROI (6 mm) centered on the peak voxel of a cluster demonstrating an effect of scene type (food vs. control) in the whole-brain analysis. For regions involved in representing the value of food items (i.e., OFC, ventral striatum), the alpha level for ROI analyses was .05. For all other areas, subsequent between-group analyses were Bonferroni corrected for the total set of ROIs examined (i.e., $\alpha = .003$). As the depleted and control groups contributed equally to the ROI-defining statistical map, the ROIs are considered statistically unbiased with regard to between-group effects.

To measure depletion-related differences in functional connectivity, we conducted separate psychophysiological interaction (PPI) analyses (Friston et al., 1997) for the OFC and striatum. In each analysis, the first eigenvariate of the time series of voxels within the seed ROI (OFC or striatum) was deconvolved from the HRF in order to generate an estimated neuronal time series (Gitelman, Penny, Ashburner, & Friston, 2003), which was then multiplied by a vector coding for the psychological context (i.e., food vs. control trials) and reconvolved with the HRF. This new predictor was entered into a GLM along with the psychological-context vector, the original eigenvariate time series for the seed region, and covariates of no interest (the same as in the preceding analysis). Parameter estimates for the PPI interaction term at the IFG were tested to determine whether the depleted and control groups differed in context-dependent (food vs. control trials) connectivity.

Results

Behavioral results

The depleted and control groups did not differ in their reaction times on the incidental judgment task (indoor vs. outdoor), both on food trials (depleted: $M = 1,038$ ms; control: $M = 1,019$ ms), $t(27) = 0.29$, $p = .78$, and on control trials (depleted: $M = 995$ ms; control: $M = 921$ ms), $t(27) = 1.47$, $p = .15$. Participants in the depleted group scored higher on the subjective measure of cognitive depletion than did participants in the control group (depleted: $M = 3.9$; control: $M = 2.7$), $t(29) = 2.81$, $p = .009$.

Brain regions demonstrating food-cue-related activity and their association with ratings of food liking

Whole-brain random-effects analysis of the food-versus-control contrast across both groups revealed greater food-cue-related activity in the left OFC, right ventral striatum, and bilateral insula, among other regions (Fig. 1, Table 2). ROI analysis revealed that participants' liking for each food item was a significant modulator of activity in the OFC during food trials, $t(30) = 2.07$, $p = .047$ (mean $\beta = 0.07$), and a marginally significant modulator of activity in the ventral striatum during food trials, $t(30) = 1.98$, $p = .056$ (mean $\beta = 0.05$). (Note that the β

represent the increase in signal change per unit of the parametric modulator, i.e., food liking.)

Brain regions differentiating the depleted and control groups

ROI analysis on regions derived from the food-versus-control contrast revealed that depleted participants demonstrated greater food-cue-related activity in the left OFC than did control participants, $t(29) = 2.20$, $p = .036$ (Fig. 2a). The right ventral striatum ROI demonstrated the same pattern of greater food-cue-related activity in depleted participants, but the between-group difference was not significant, $t(29) = 1.37$, $p = .18$ (Fig. S2 in the

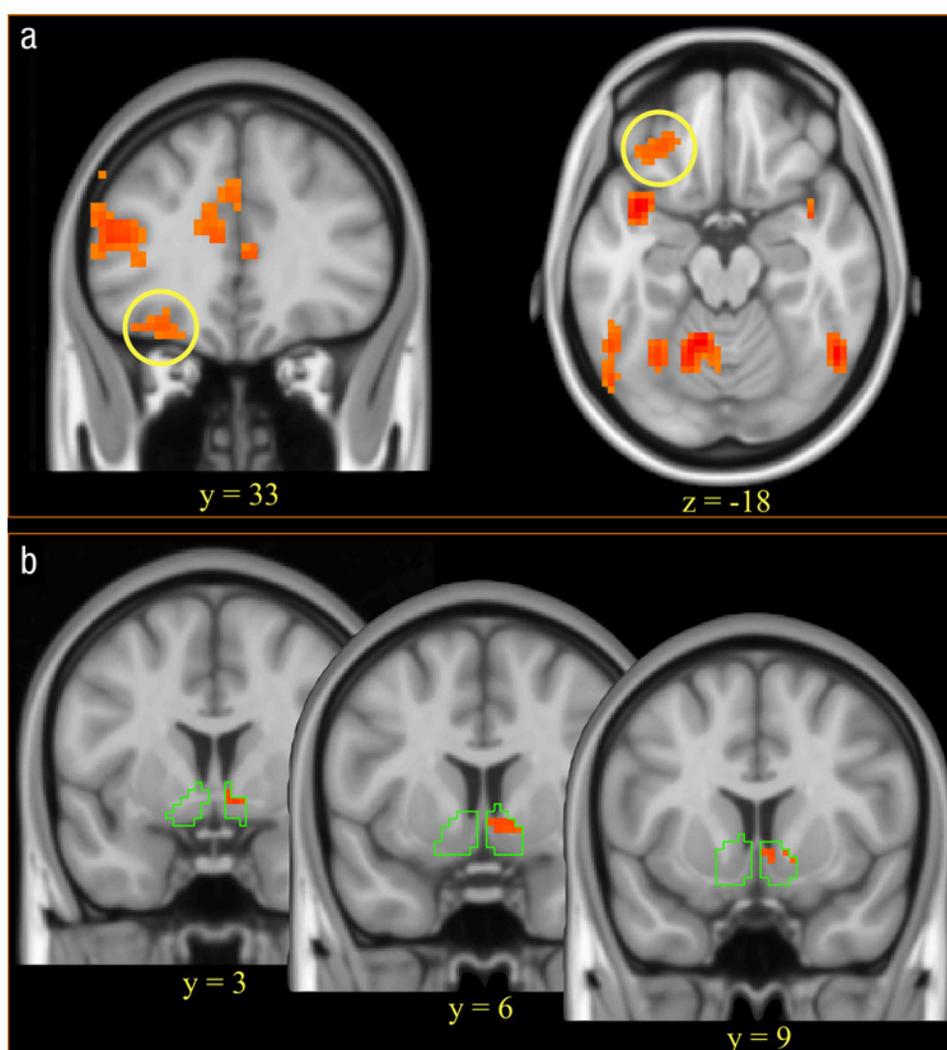


Fig. 1. Brain regions demonstrating greater reactivity to food trials than to control trials (natural scenes) across the depleted and control groups ($p < .05$, corrected). In (a), the yellow circle on the coronal and axial planes indicates the location of the left orbitofrontal cortex. The images in (b) show the location of food-cue-related activity in a region of the ventral striatum/nucleus accumbens ($p < .05$, corrected for the volume of the nucleus accumbens). The green outline demarcates the borders of the anatomical volume of the nucleus accumbens that was used for small-volume correction.

Table 2. Brain Regions Demonstrating Greater Activity in Response to Food Images Than in Response to Control (Natural) Scenes Across All Participants

Brain region	Side	BA	$t(30)$	Coordinates of peak activation		
				x	y	z
Orbitofrontal cortex	Left	11	4.48	-30	33	-18
Ventral striatum	Right	—	3.51	9	3	-6
Superior temporal gyrus	Left	38	7.41	-39	3	-15
Insula ^a	Left	13	5.96	-39	-6	3
Inferior frontal gyrus ^a	Left	45	5.60	-45	24	18
Insula	Right	13	6.53	45	-6	0
Posterior cingulate cortex	Right	23	8.85	42	-21	24
Supplementary motor area	Left	6	5.82	-9	15	63
Supplementary motor area ^a	Left	6	4.97	-9	15	54
Dorsal anterior cingulate cortex ^a	Left	32	4.92	-6	24	36
Supplementary motor area	Right	24	5.30	12	-9	54
Fusiform	Right	37	6.48	51	-60	-18
Superior parietal lobule	Left	7	5.58	-36	-66	54
Inferior parietal lobule ^a	Left	19	5.37	-33	-69	42
Lingual gyrus	Left	18	8.37	-9	-94	-6
Middle occipital gyrus	Left	37	5.38	-42	-66	-9
Cerebellum	Left	—	11.31	-21	-51	-30
Thalamus	Right	—	4.92	15	-21	3

Note: The table reports the locations of peak voxels for significant clusters ($p < .05$, corrected). Coordinates are in Montreal Neurological Institute stereotaxic space. BA = Brodmann's area (approximate).

^aRow labels that are indented refer to local maxima at least 8 mm distant from the peak voxel within the corresponding cluster.

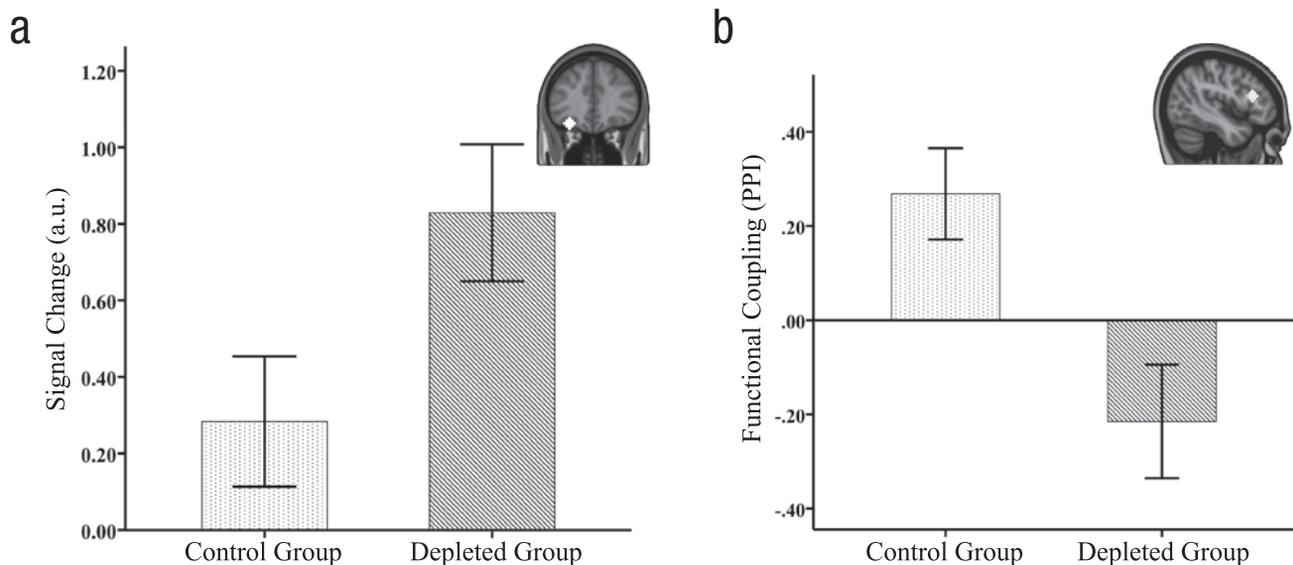


Fig. 2. Between-group differences in (a) food-cue-related reactivity (food trials vs. control trials) in the left orbitofrontal cortex (OFC; see the inset) and (b) context-dependent (food trials vs. control trials) functional connectivity between the left OFC and left inferior frontal gyrus (IFG; see the inset). The left OFC and left IFG regions of interest were defined in an unbiased manner from the comparison of food and control trials across both the depleted and the control groups. Error bars indicate ± 1 SEM. a.u. = arbitrary units.

Supplemental Material). For the sake of completeness, we note that three regions that were not hypothesized to show a group difference for this contrast did show a significant difference at an uncorrected α of .5: left middle occipital gyrus ($p = .047$) and the insula bilaterally (left insula: $p = .042$; right insula: $p = .036$). However, these regions did not show a group effect after correction for the total set of ROIs (see the Method section). No other ROI exhibited a significant depletion effect at either the corrected or the uncorrected level.

Differential functional connectivity of the OFC and ventral striatum with the IFG

Analysis of context-dependent (i.e., food vs. control trials) functional connectivity between the left OFC and the left IFG ROI defined from the food-versus-control contrast (see Table 2 for coordinates) revealed reduced context-dependent connectivity between these two regions in depleted compared with control participants, $t(29) = 3.10$, $p = .004$ (Fig. 2b; for representative plots from individual participants, see Fig. S3 in the Supplemental Material). Separate analysis of each group demonstrated a significant positive context-dependent coupling in the control group, $t(14) = 2.77$, $p = .015$, but no differential connectivity in the depleted group, $t(15) = 1.79$, $p = .094$.

A similar between-group difference in context-dependent functional connectivity was found for the ventral striatum and the left IFG, $t(29) = 2.04$, $p = .05$. Although we did not observe recruitment of the right IFG in the whole-brain analysis of task effects, given the strong theoretical prediction that the right IFG would be involved in inhibition and cognitive control (see the Discussion section), we repeated the analysis using a right IFG ROI generated by mirroring the center coordinates of the left IFG ROI along the x -axis (i.e., Montreal Neurological Institute coordinates: $x = 45$, $y = 24$, $z = 18$). This right IFG ROI similarly showed reduced context-dependent functional connectivity with both the OFC, $t(29) = 3.16$, $p = .004$ and the ventral striatum, $t(29) = 2.73$, $p = .01$, in depleted compared with control participants.

Correlation between OFC activity in response to food images and self-reported depletion

Analyses revealed a significant relationship between food-cue-related activity in the left OFC and the self-report index of depletion in the depleted group ($r = .591$, $p = .016$), but not in the control group ($r = -.04$, $p = .89$). Moreover, a moderated regression analysis (for more details, see Supplementary Results in the

Supplemental Material) revealed that participant group was a marginally significant moderator of the relationship between self-reported depletion and OFC activity, $\beta_{\text{Group} \times \text{Self-Reported Depletion}} = 0.331$, $p = .051$ (Fig. 3).

Discussion

The ability to inhibit responding to temptations fluctuates with prior exertion of self-control (Baumeister & Heatherton, 1996). Until recently, strength theories of self-regulation have generally assumed that self-regulatory depletion reduces the capacity for self-control but does not affect the intensity of impulses and desires. For example, Vohs and Heatherton (2000) demonstrated that dieters overeat following exertion on a self-control task. At the time, the authors interpreted this finding as resulting from weakened self-control rather than increased desire. Recent research, however, suggests that impulses and desires are themselves subject to modulation when people are in a depleted state (i.e., Schmeichel et al., 2010; Vohs et al., 2012). The current study demonstrated that prior exertion of self-regulatory effort alters the neural processing of a primary reward—in this case food—resulting in an exaggerated response to food items in the OFC. Consistent with the idea that there are individual differences in the capacity to engage in self-control (e.g., Baumeister & Heatherton, 1996; Hagger et al., 2010), our study also showed that activity in the OFC during food-cue exposure is correlated with individuals' self-reported degree of depletion. The OFC has been consistently implicated in food-cue-reactivity studies (for a meta-analysis, see Van der Laan et al., 2011) and has been

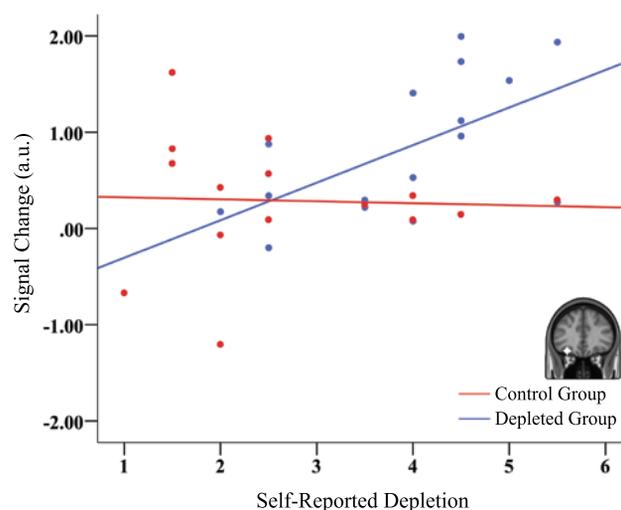


Fig. 3. Scatter plot (with best-fitting regression lines) of food-cue-related activity in the left orbitofrontal cortex as a function of self-reported depletion in the depleted and control groups. a.u. = arbitrary units.

shown to code for the subjective liking and pleasantness of foods, as demonstrated in the current study with food cues as well as in a prior study examining actual food consumption (Kringelbach et al., 2003). Finally, a similar pattern of exaggerated response to food cues following depletion was found in the ventral striatum; however, the magnitude of response in this region failed to differentiate between depleted and control participants (see Fig. S2).

In addition to finding differences in food-cue-related activity in the OFC, we found that depleted participants exhibited reduced functional connectivity of the OFC and ventral striatum with both the left and the right IFG. Although the right IFG is more commonly implicated in inhibitory control (Aron, Robbins, & Poldrack, 2004), particularly inhibiting motor responses such as during go/no-go tasks (Somerville et al., 2011), the left IFG has also been implicated in response inhibition (e.g., Li, Huang, Constable, & Sinha, 2006) and in indexing the subjective evaluation of the cognitive costs of performing an action (McGuire & Botvinick, 2010). Moreover, the left IFG is involved in the regulation of emotion (McRae et al., 2010), as well as food and cigarette cravings (Kober et al., 2010), and increased activity in this region, along with the right IFG, during a response-inhibition task predicts subsequent weakening of the relationship between craving and real-world smoking behavior (Berkman et al., 2011). Finally, activity in the left IFG is increased when dieters make healthy choices when deciding between healthy and unhealthy foods (Hare et al., 2009).

Considered together with the current findings, the available data offer partial support for a model in which self-regulation is sustained by the balance between activation of prefrontal brain regions involved in executive control and activation of brain areas involved in representing motivational salience and reward value. However, it is important to note that this interpretation rests on the observation of reduced functional connectivity between the IFG and OFC and between the IFG and striatum in depleted participants compared with control participants. We note that the analysis of context-dependent functional connectivity provides information that can be used to make inferences about interregion communication. Thus, one interpretation of these findings is that nondepleted dieters engage in self-regulation when viewing tempting food scenes and that this is manifest as a positive functional coupling between IFG and OFC during food scenes relative to control scenes. Depletion appears to disrupt the functional connectivity between these countervailing systems such that these regions become uncoupled in the face of temptations; thus, in depleted participants, there is little or no difference in IFG-OFC connectivity between food and control trials (see the Results section). Taken together, our findings suggest that

depleted participants show an increased response to tempting food because of the reduced coupling between IFG and OFC; however, further research is needed to test whether depletion-induced changes in functional connectivity mediate changes in food-cue-related activity.

In the present study, we kept chronic dieters naive to the nature of the study and to their special status as dieters by employing a simple categorization task. Although they were not explicitly instructed to regulate their responses to appetizing food items, we expected that they would engage in some degree of self-regulation, given that restricted eating is one of the central features defining this population (Vohs & Heatherton, 2000). We therefore suggest that the observed group difference in differential connectivity of the OFC and striatum with the IFG likely reflects a failure among depleted dieters to restrain their responses to appetizing food cues. However, research using explicit regulation paradigms (as in Kober et al., 2010) is needed to further examine this claim.

A limitation of this study is that we restricted our participant sample to include only chronic dieters. An open question is whether nondieters would show increased food-cue reactivity following depletion. We note that previous studies of nondieters have indicated robust reward-related brain activity in response to food cues in the absence of any experimental manipulations (e.g., Demos et al., 2011). Although both chronic dieters and nondieters show evidence of food-cue-related brain activity, we suggest that only dieters, by virtue of their tonic restraint, would show an exaggerated reward response to food cues following depletion.

The current findings complement recent behavioral work showing that self-regulatory depletion intensifies impulses and emotions (Vohs et al., 2012) and also guides attention toward rewarding cues (Schmeichel et al., 2010). Moreover, these findings are consistent with work showing that when dieters are in a "hot" affective state, they show stronger hedonic responses to food than nondieters do (Hofmann, Van Koningsbruggen, Stroebe, Ramanathan, & Aarts, 2010; Papies, Stroebe, & Aarts, 2007). Our findings also complement a recent study investigating the effects of self-regulatory depletion in the emotional domain (Wagner & Heatherton, 2012). In that study, participants underwent the same attention-control task as used here, but were subsequently exposed to emotional scenes. Compared with nondepleted participants, depleted participants showed greater activity in the amygdala, a brain region implicated in emotional evaluations, when viewing negative scenes. Moreover, depleted participants also exhibited reduced functional connectivity between the amygdala and the ventromedial prefrontal cortex, a region often implicated in regulating emotional responses (e.g., Somerville et al., 2013). Thus, together with the present findings, these results offer

neural evidence that temptations and emotional experiences are intensified when people are in a depleted state.

Since its inception, the strength model of self-regulation has had considerable influence on theories of self-control failure (Hagger et al., 2010). Nevertheless, recent accounts have raised questions about how depletion leads to such failure. In the current study, self-regulatory depletion increased neural responses to appetizing food cues in brain regions involved in representing the reward value of food and simultaneously decreased the functional coupling between these areas and lateral prefrontal regions important for cognitive control. These results support a balance model of self-regulation (e.g., Heatherton & Wagner, 2011) and suggest that in situations in which people are highly motivated to restrain or otherwise moderate their behavior, impaired recruitment of the lateral prefrontal cortex may serve to release the brain's motivation and reward systems from inhibition. Such a release may result in increased reward sensitivity when people are confronted with temptations, which may then impel them to act on their desires, ultimately resulting in self-regulation failure.

Author Contributions

All authors designed the experiment. M. Altman and R. G. Boswell collected the data. D. D. Wagner and M. Altman analyzed the data. D. D. Wagner, M. Altman, W. M. Kelley, and T. F. Heatherton interpreted the data. D. D. Wagner wrote the first draft of the manuscript. T. F. Heatherton contributed to the final version of the manuscript. All authors approved the final version for submission.

Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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Supplemental Material

Additional supporting information may be found at <http://pss.sagepub.com/content/by/supplemental-data>

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