

ARTICLE



Reducing reward responsivity and daily food desires in female dieters through domain-specific training

Pin-Hao A. Chen ^a, William M. Kelley^a, Richard B. Lopez^b and Todd F. Heatherton^a

^aDepartment of Psychological and Brain Sciences, Dartmouth College, Hanover, NH; ^bDepartment of Psychology, Rice University, Houston, TX

ABSTRACT

According to the strength model, self-regulation relies on a domain-general capacity that may be strengthened by training. From this perspective, training self-regulation in one domain may transfer to other domains. Here we used two inhibitory training paradigms, a domain-general and domain-specific stop-signal training task and compared their effects on brain reward activity as well as daily food desires in female dieters. Before and after the training, functional magnetic resonance imaging was used to assess food cue-reactivity, coupled with one week of smart-phone ecological momentary assessments to examine eating urges. Whereas the food-specific inhibitory training was successful in reducing both food cue-reactivity and food desires, the domain-general (sound-cue) training showed no transfer effects. These findings suggest that domain-specific training may be a more effective method for supporting self-regulation than domain-general approaches aimed at strengthening self-regulation across domains.

ARTICLE HISTORY

Received 10 January 2018
Revised 18 May 2018
Published online 31 August 2018



KEYWORDS

Food; desire; reward;
self-control; training;
neuroimaging

Introduction

The strength model is based on the proposition that successful self-regulation relies on a domain-general resource (Baumeister, Vohs, & Tice, 2007; Baumeister & Heatherton, 1996). According to this model, self-regulatory capacity is a limited resource that varies among people, that can be depleted by effort exertion, and perhaps optimistically that may be strengthened by repeated practice (Baumeister, Bratslavsky, & Muraven, 1998; Hagger, Wood, Stiff, & Chatzisarantis, 2010). Although data have recently emerged questioning the generality of depletion effects across all dependent measures (Collaboration, 2015), considerable evidence has emerged over the last 20 years demonstrating reliable depletion effects across many domains (Freeman & Aron, 2016; Heatherton & Wagner, 2011; Vohs, Baumeister, & Ciarocco, 2005). To the extent that self-regulatory strength is a domain general resource, one might expect that training would transfer across domains (Berkman, Graham, & Fisher, 2012; Muraven, Baumeister, & Tice, 1999). Such a strengthening of self-regulatory resources could help prevent self-regulation failures, which are implicated in many behaviors that threaten mental or physical health (i.e. drug addiction, emotion regulation, and obesity). However, to date, little evidence is available on whether self-regulation can be trained.

The strength model has been used to examine self-regulatory failure, such as when chronic dieters give in to temptation and overeat. Previous research has demonstrated that although people can diet successfully over the short-term, diet failure is common with frequent bouts of overeating (Wagner & Heatherton, 2015). For example, one study used a domain general emotion-regulation task to deplete self-regulatory strength and found that dieters ate more when depleted than in the control condition (Vohs & Heatherton, 2000). More recently, Wagner and colleagues (Wagner, Altman, Boswell, Kelley, & Heatherton, 2013) found that a domain-general inhibitory task led to heightened brain reward activity among depleted chronic dieters. An open question is whether this resource can be strengthened through practice or training. To the extent that domain general depletion tasks have been shown to produce self-regulation failures across several behaviors, one might expect self-regulatory training to strengthen this system in a domain-general fashion. Conversely, it seems plausible that the best way to control a specific behavior is to engage in domain-specific training for that behavior (Veling, Aarts, & Papies, 2011; Veling, Aarts, & Stroebe, 2013). The former would be more advantageous as it would permit a single training approach to benefit a broad spectrum of behavior. However, the literature is mixed on such effects. Indeed, although some pre-

CONTACT Pin-Hao A. Chen  pin-hao.chen.gr@dartmouth.edu  Department of Psychological and Brain Sciences, Dartmouth College, 6207 Moore Hall, Hanover, NH, 03755

 supplemental data for the article can be accessed [here](#)

© 2018 Informa UK Limited, trading as Taylor & Francis Group

vious attempts to examine this domain-transfer hypothesis have revealed supportive evidence (Bertrams & Schmeichel, 2013; Finkel, DeWall, Slotter, Oaten, & Foshee, 2009; Gailliot, Plant, Butz, & Baumeister, 2007; Hui et al., 2009; Muraven, 2010), recent reviews on either working memory or executive control training are more equivocal (Melby-Lervåg & Hulme, 2013; Melby-Lervåg, Redick, & Hulme, 2016; Owen et al., 2010).

The goal of the present study was to examine whether domain-general or domain-specific training affects food cravings and accompanying reward responsivity in chronic dieters. To do so, we used a stop-signal paradigm and trained one group of chronic dieters to inhibit to domain-general sound cues and another group of dieters to inhibit to domain-specific, appetizing food cues. Prior to and after training, participants were assessed for food cue-reactivity during event-related fMRI scanning; based on prior studies of food cue-reactivity, we were interested in examining brain responsivity to appetizing food cues in the reward system, particularly the ventral striatum (VS) and orbitofrontal cortex (OFC). In addition, we also examined food-cue responsivity in the frontoparietal (FP) control system, which has been shown to implement aspects of cognitive control (Dosenbach et al., 2007; Petersen & Posner, 2012; Petersen & Sporns, 2015; Power et al., 2011). Participants also completed a week of ecological momentary assessments (EMA) so that we could not only examine the effects of training on brain activity, but also on daily self-regulatory behaviors. We hypothesized that self-regulatory training would be effective in reducing food-cue responsivity in the reward system as well as in changing self-regulatory behaviors. An open question is whether domain-general training would be as effective as domain-specific training.

Methods

Participants

Forty-two right-handed female chronic dieters were recruited from a large sample of undergraduate

students who completed the Restraint Scale, a validated questionnaire to measure individual differences in chronic dieting tendencies (Heatherton, Herman, Polivy, King, & McGree, 1988). Participants were considered chronic dieters only when their scores were higher than 16 on the Restraint Scale (Heatherton, Polivy, & Herman, 1991). Participants in the two training groups did not differ across demographic or dieting characteristics before training (Table 1). All participants had a negative history of mental health disorders or neurological problems. Six participants were excluded from analysis due to excessive head motion (i.e. more than 3 mm in either x-, y – or z-direction) during the scanning sessions, leaving a total of 36 participants (18 in each training group). Participants were randomly assigned to one of two groups, receiving either food-cue inhibitory training or sound-cue inhibitory training. Participants gave informed consent in accordance with the guidelines set by the Committee for the Protection of Human Subjects at Dartmouth College.

Procedure overview

The current study contained five phases that spanned 28 days total: (1) pre-training (baseline) fMRI session, (2) pre-training (baseline) EMA sampling, (3) training period, (4) post-training fMRI session, and (5) post-training EMA sampling (Figure 1).

Following the pre-training fMRI session, participants were asked to answer eating-related questions seven times per day for one week via their smartphones. After this baseline data collection period, participants were randomly assigned to participate in either the domain-general, sound-cue inhibitory training program or the domain-specific food-cue inhibitory training program. The training started one or two days after the pre-training experience-sampling phase and lasted for ten sessions. Each session lasted 30 minutes, and participants finished these 10 sessions within 12 days. One or two days after the training, the post-training fMRI session took place, which followed the same procedure as the pre-training fMRI session. This was then followed by

Table 1. Demographic and dieting characteristics in the pre-training and post-training fMRI session.

Measurement	Food-cue inhibitory training group	Sound-cue inhibitory training group
Pre-training fMRI session		
Age (years)	19.22 (1.26)	18.88 (1.27)
BMI (kg/m ²)	23.19 (2.65)	21.80 (2.02)
Hours slept the previous night	7.47 (1.27)	6.63 (1.44)
Current hunger before scanning	2.55 (0.92)	3.16 (1.72)
Restraint Scale scores	20.16 (3.39)	20.05 (4.47)
Post-training fMRI session		
BMI (kg/m ²)	23.21 (2.97)	21.91 (1.85)
Hours slept the previous night	7.30 (1.68)	7.02 (0.96)
Current hunger before scanning	3.33 (1.71)	3.11 (1.64)

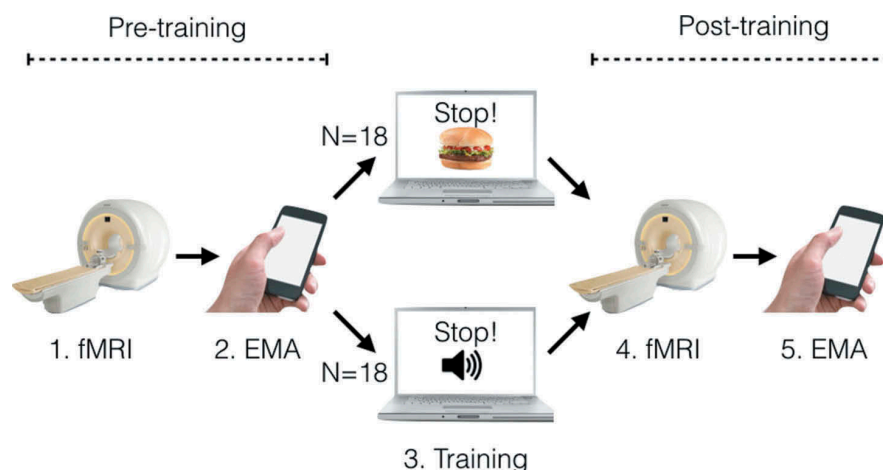


Figure 1. Study design. (1) Pre-training (baseline) fMRI session. (2) Pre-training (baseline) EMA sampling period. (3) Training period. (4) Post-training fMRI session. (5) Post-training EMA sampling period.

another week of post-training experience-sampling. Participants were debriefed with the study purpose upon completion of all five phases.

Procedure in the pre – and post-training fMRI sessions

Before each fMRI session, participants were asked to refrain from eating or drinking for at least two hours. For each fMRI session, participants first performed a depleting inhibitory control task (Wagner & Heatherton, 2012), which was immediately followed by a food-cue reactivity task used in our prior studies (Demos, Heatherton, & Kelley, 2012; Lopez, Hofmann, Wagner, Kelley, & Heatherton, 2014; Wagner et al., 2013; Wagner, Boswell, Kelley, & Heatherton, 2012). In the depletion inhibitory control task, participants were asked to view a seven-minute video about Canadian bighorn mountain sheep. Throughout the video, a series of distractor words (40 in total) that appeared at the bottom of the screen and moved to the center within three seconds. Participants were instructed to refrain from reading these distractor words and to maintain focus on the video. The depletion inhibitory control task is necessary to elicit robust food-cue reward responses in dieters because in neutral conditions, dieters tend to show relatively little food-cue reactivity (Wagner et al., 2013).

The food-cue reactivity task was adapted from previous studies (Demos et al., 2012; Wagner et al., 2013, 2012), using 90 appetizing food images, and another 180 images involving people or natural scenes taken as control images. In this event-related task, each image was presented for 2000 ms, followed by a fixation for another 500 ms, and jittered between 0 to 5000 ms. The order of image presentation was pseudo-randomized. In this task, participants

made perceptual (indoor/outdoor) judgments about the images, which ensured that participants remained alert and naive to the purpose of the study.

Experience sampling administration

Following the pre-training fMRI session, participants were instructed on how to respond to experience-sampling signals via their own smartphones immediately after the pre-training fMRI session. The signals were distributed by an SMS survey distribution application (SurveySignal) developed by Hofmann and colleagues (Hofmann & Patel, 2015).

Both pre-training and the post-training experience-sampling periods lasted seven days. Seven signals were sent in a 14-hr time window from 9 a.m. to 11 p.m. This window was divided into seven two-hour time blocks, with each signal sent randomly in each block. The interval between signals was set to be at least 30 minutes. If a participant did not respond within 15 minutes, SurveySignal would send out a reminder text message. If the participant still did not respond, the link would expire after ten minutes, and this signal was recorded as missing data.

For each signal, participants replied to a series of questions. They were asked if they had desired food within the past 30 minutes (i.e. the presence of a food desire), and if so to rate the strength of that desire (desire strength) on a scale from one to six. Regarding the overall percentage of signal responses, there was a slight difference between groups during the pre-training experience-sampling period (food-cue training group: 72.1%; sound-cue training group: 62.4%; $t(34) = 2.18$, $p = 0.035$), but no difference was observed during the post-training period (food-cue training group: 61.1%; sound-cue training group: 57.0%; $t(34) = 0.58$, $p = 0.565$).

Domain-general sound-cue inhibitory training vs. domain-specific food-cue inhibitory training

Both training programs consisted of 10 sessions over the course of two weeks, with five sessions scheduled each week. Participants were asked to complete four blocks of the inhibitory training on each session. The only difference between the two training programs was the cue presented as the stop signal. Participants in the domain-general sound-cue training group received the classical stop-signal task with an auditory cue signaling stop (Berkman, Kahn, & Merchant, 2014; Verbruggen & Logan, 2008). By contrast, participants in the domain-specific food-cue training group were asked to withhold pressing the button when they saw an appetitive food image on the screen.

Each block of this task consisted of 128 trials, and 32 of these trials were stop trials. Each trial started with a cue (500 ms), followed by a go signal with an arrow pointing either to the left or right side (1000 ms). Participants in both training groups were instructed to press the left or right arrow key as quickly as possible when they saw the go signal on the computer screen and to withhold pressing the button when they received their respective stop signals. The inter-trial duration was jittered with a gamma distribution (mean = 1400 ms) and varied across trials. The stop signal delay (SSD) was designed to be adjustable in a 50 ms interval with a staircase function, depending upon whether participants successfully withheld pressing the button. Two independent staircases, starting at 200ms and 300ms, were used to alternately adjust the SSD to achieve 50% response accuracy for the stop trials. Beginning on the second block, the SSD value in the block was set as the estimated SSD from the prior block. This continuously adaptive design adjusted the level of difficulty across trials.

For each of the food-cue inhibitory training blocks, eight appetitive food images were chosen to serve as stop signals, and each image was repeated four times in each block. The same food images were used on the same training day, but different food images were used across ten training days. These food images were selected from a normed food image dataset (Blechert, Meule, Busch, & Ohla, 2014) and were distinct from the food images in the fMRI food-cue reactivity task. Since this dataset provided several ratings about food items in each image, we selected 80 food images from this dataset with high calories (above 120 kcal/100g) and high ratings on palatability and craving (above 6.1 out of a ten-point rating scale). These images were divided into 10 sets, and these 10 sets were used on the 10 training sessions in the food-cue inhibition-training program without repetition.

A critical measure in this task was the stop-signal reaction time (SSRT), which was calculated based on the difference between the median reaction time among the go trials and the SSD. The SSRT was computed separately for each block and averaged across the four blocks in each training session. This averaged SSRT was taken as the index representing the performance in both of the food-cue and sound-cue inhibitory training task. The difference in average SSRT collected in the first training session and the last training session was used as the improvement index of inhibition training.

Image processing and analysis

Participants were scanned in a Philips Intera Achieva 3T scanner with a thirty-two channel head coil. Structural images were acquired by using a T1-weighted MP – RAGE sequence (160 sagittal slices, TR = 9.9 ms, TE = 4.6 ms, 8 flip angles, $1 \times 1 \times 1$ mm voxels). Functional images were acquired using a T2*-weighted echo-planar sequence (TR = 2,500 ms, TE = 35 ms, 90 flip angle, FOV = 240 mm, 36 axial slices, 3 mm thick with 0.5 mm gap, 3×3 mm in-plane resolution).

fMRI were analyzed using SPM8 (Wellcome Department of Cognitive Neurology, London, England) in conjunction with a toolbox for preprocessing and analysis (available at <http://github.com/ddwagner/SPM8w>). Within each functional run, differences in acquisition time between slices were first corrected. Images were then realigned within and across functional runs by the affine registration with 6 DOFs for motion correction. After motion correction, images were unwarped to decrease residual motion-related distortions which were not corrected previously. Next, images were normalized into a standard stereotaxic space (3x3x3mm isotropic voxels), SPM8 EPI template, which conforms to the ICBM 152 brain template space. Lastly, a 6-mm full-width-at-half-maximum Gaussian kernel was applied for spatial smoothing. For each participant, a general linear model incorporating task effects and covariates of no interest (a session mean, a linear trend to account for low-frequency drift, and six movement parameters derived from realignment corrections) was computed and convolved with a canonical hemodynamic response function (HRF). We first created contrast images comparing food and control images in the pre-training fMRI session, and then repeated the same procedure for the post-training fMRI session for each participant. These contrast images were subsequently entered into a second-level, random-effects analysis.

Targeted reward ROI analysis

Region-of-interest (ROI) analyses were done in two key reward regions, the VS and the OFC. To obtain a VS and an OFC ROI in an unbiased manner, a spherical VS ROI (9, 3, -6; 6 mm radius) and a spherical OFC ROI (-30, 33, -18; 6 mm radius) were defined based on a previous study of reward using the same cue-reactivity paradigm on the same scanner (Wagner et al., 2013). Because this previous study also used the same food-cue reactivity task in chronic dieters, these coordinates may reliably represent peak coordinates in an unbiased way. For each ROI, parameter estimates of beta values for the contrast of food-vs.-control images were extracted and entered into a two (group: food-cue training, sound-cue training) by two (time: pre-training, post-training) ANOVA.

Reward and control system analysis

A second analysis investigated the relationship between motivation and self-regulatory control at systems level; prior work has demonstrated that the balance between reward and control activity may be a better predictor of self-regulatory outcomes (Chen, Chavez, & Heatherton, 2017; Lopez et al., 2017), and recent advances in fMRI data analysis has permitted identification and characterization of functionally correlated brain systems (Huckins et al., 2018). Region-of-interests (ROIs) from two systems, a reward system consisting of nine ROIs and a frontoparietal (FP) control system consisting of 29 ROIs were chosen from a recent study applying graph theory approaches to a large cohort ($N = 858$) of resting-state functional connectivity (RSFC) data (Table 2; Huckins et al., 2018). Regions comprising the FP control system shared near identical overlap with previously published graph theoretical analyses of RSFC data (Power et al., 2011). Within each system, parameter estimates of signal change for the contrast of food-vs.-control images were extracted from each ROI. An aggregated mean signal change across all ROIs was then computed for each system and entered into a two (group: food-cue training, sound-cue training) by two (time: pre-training, post-training) ANOVA.

EMA data analysis

Two measures were used to assess participants' daily eating patterns (Lopez et al., 2014): percentage of food desires and average desire strength. These two measures were computed for the pre-training and post-training experience-sampling period separately. Each measure was then analyzed in an ANOVA design with one between-subject factor (training group: food-cue

training, sound-cue training) and one within-subject factor (time: pre-training, post-training).

Results

SSRT results

Both the domain-specific food-cue training group and the domain-general sound-cue training group showed significant improvement in the SSRT following training (Main effect of time: $F(1, 34) = 28.1, p < 0.001, \eta_p^2 = 0.45$; food-cue group: pre-training $M = 267.8$ ms; post-training $M = 202.8$ ms; $t(17) = 3.5, p = 0.002, d = 1.21$; sound-cue group: pre-training $M = 241.2$ ms; post-training $M = 199.7$ ms; $t(17) = 5.8, p < 0.001, d = 1.01$). Importantly, improvements did not differ across groups (Main effect of training group, $F(1, 34) = 1.5, p = 0.2, \eta_p^2 = 0.04$; group x time interaction effect, $F(1, 34) = 1.4, p = 0.25, \eta_p^2 = 0.03$). Behavioral performance across all tasks is summarized in Table 3.

EMA results for daily food desires

In order to determine which type of training could effectively reduce dieters' food desires, we compared both training groups by using two EMA measure (percentage of food desires and average desire strength). Before training, the two groups did not differ in their percentage of food desires, $t(34) = -0.14, p = 0.89, d = -0.08$. Following training, participants in the food-cue training group reported a greater reduction in food desires (pre-training: $M = 36.12\%$; post-training: $M = 27.91\%$; $t(17) = 2.8, p = 0.011, d = 0.44$) than participants in the sound-cue training group (pre-training: $M = 36.75\%$; post-training: $M = 37.91\%$; $t(17) = -0.4, p = 0.687, d = -0.02$): group x time interaction, $F(1, 34) = 5.3, p = 0.03, \eta_p^2 = 0.13$ (Figure 2a).

Similarly, before training, the two training groups did not differ in their average food desire strength, $t(34) = 0.15, p = 0.59, d = 0.21$. Following training, participants in the food-cue training group also reported a reduction in average food desire strength (pre-training: $M = 4.05$; post-training: $M = 3.26$; $t(17) = 2.6, p = 0.02, d = 0.76$) whereas those in the sound-cue training group did not (pre-training: $M = 3.98$; post-training: $M = 3.92$; $t(17) = 0.3, p = 0.80, d = 0.23$): group x time interaction, $F(1, 34) = 3.7, p = 0.06, \eta_p^2 = 0.10$ (Figure 2b).

Neuroimaging results: training effect on reward activity in the VS and OFC

Before training, the food - and sound cue-training groups did not differ in brain responsivity to food

Table 2. Peak coordinates for Reward and Fronto-parietal control systems identified using RSFC in a cohort of 858 subjects (Huckins et al. 2018).

System	MNI Coordinates			Anatomical Location
	x	y	z	
Fronto-parietal	-53	-49	43	Inferior parietal lobule
Fronto-parietal	55	-45	37	Supramarginal gyrus
Fronto-parietal	-27	-71	37	Precuneus
Fronto-parietal	48	25	27	Inferior frontal gyrus – pars triangularis
Fronto-parietal	47	10	33	Precentral gyrus
Fronto-parietal	-41	6	33	Precentral gyrus
Fronto-parietal	38	43	15	Middle frontal gyrus
Fronto-parietal	49	-42	45	Inferior parietal lobule
Fronto-parietal	-28	-58	48	Inferior parietal lobule
Fronto-parietal	44	-53	47	Inferior parietal lobule
Fronto-parietal	32	14	56	Middle frontal gyrus
Fronto-parietal	37	-65	40	Angular gyrus
Fronto-parietal	-42	-55	45	Inferior parietal lobule
Fronto-parietal	-34	55	4	Middle frontal gyrus
Fronto-parietal	-42	45	-2	Middle frontal gyrus
Fronto-parietal	33	-53	44	Inferior parietal lobule
Fronto-parietal	43	49	-2	Middle frontal gyrus
Fronto-parietal	-42	25	30	Inferior frontal gyrus – pars triangularis
Fronto-parietal	-23	11	64	Superior frontal gyrus
Fronto-parietal	58	-53	-14	Inferior temporal gyrus
Fronto-parietal	-3	26	44	Superior medial frontal gyrus
Fronto-parietal	-56	-45	-24	Inferior temporal gyrus
Fronto-parietal	-47	-51	-21	Inferior temporal gyrus
Fronto-parietal	-48	38	14	Inferior frontal gyrus
Fronto-parietal	48	40	11	Inferior frontal gyrus – pars triangularis
Fronto-parietal	-48	8	29	Precentral gyrus
Fronto-parietal	-57	-56	-12	Inferior temporal gyrus
Fronto-parietal	-61	-38	52	Inferior parietal lobule
Fronto-parietal	-33	-46	47	Inferior parietal lobule
Reward	0	43	-7	Ventral medial prefrontal cortex
Reward	8	48	-15	Rectus gyrus
Reward	-10	16	-13	Nucleus accumbens
Reward	9	16	-13	Nucleus accumbens
Reward	23	33	-13	Orbitofrontal cortex
Reward	-24	35	-14	Orbitofrontal cortex
Reward	8	41	-24	Orbitofrontal cortex
Reward	24	45	-15	Orbitofrontal cortex
Reward	34	38	-12	Orbitofrontal cortex

Table 3. Mean behavioral responses across all training sessions presented (SD).

Session	Domain-specific training group				Domain-general training group			
	SSRT	GoRT	SSD	%Inhib	SSRT	GoRT	SSD	%Inhib
1	267.81 (34.99)	408.69 (82.82)	140.34 (99.04)	45.44 (5.30)	241.17 (29.52)	409.83 (33.66)	169.78 (52.10)	46.76 (3.48)
2	260.50 (33.89)	388.86 (39.13)	128.36 (58.19)	46.79 (4.37)	227.44 (42.03)	433.29 (89.08)	205.85 (96.42)	49.04 (2.49)
3	251.14 (34.78)	392.91 (62.11)	145.99 (70.32)	48.78 (3.09)	215.02 (38.18)	429.42 (87.34)	214.40 (98.74)	48.18 (3.84)
4	240.06 (31.58)	399.38 (51.92)	160.29 (63.49)	48.48 (3.83)	206.36 (42.15)	409.16 (69.55)	202.18 (80.01)	48.68 (1.70)
5	226.26 (46.97)	410.64 (60.89)	187.20 (79.95)	48.91 (2.49)	202.76 (46.41)	414.06 (90.19)	214.43 (100.48)	48.33 (2.47)
6	232.86 (32.03)	404.78 (43.77)	171.92 (62.33)	48.00 (3.03)	197.08 (48.83)	403.77 (71.99)	206.69 (69.63)	48.37 (1.66)
7	220.57 (51.16)	417.36 (88.08)	195.40 (111.65)	49.13 (1.75)	200.84 (50.89)	409.69 (80.97)	202.97 (63.04)	48.26 (1.77)
8	209.53 (66.85)	408.93 (81.77)	205.78 (109.51)	49.52 (3.55)	190.18 (39.41)	409.64 (76.52)	217.36 (60.33)	48.96 (1.23)
9	216.49 (56.62)	396.11 (48.15)	181.06 (72.70)	48.35 (3.07)	197.72 (49.44)	401.72 (59.64)	204.04 (59.04)	48.70 (1.34)
10	202.79 (67.39)	406.47 (68.69)	203.67 (83.68)	49.22 (3.22)	199.68 (49.77)	421.32 (80.26)	221.63 (102.44)	48.43 (3.20)

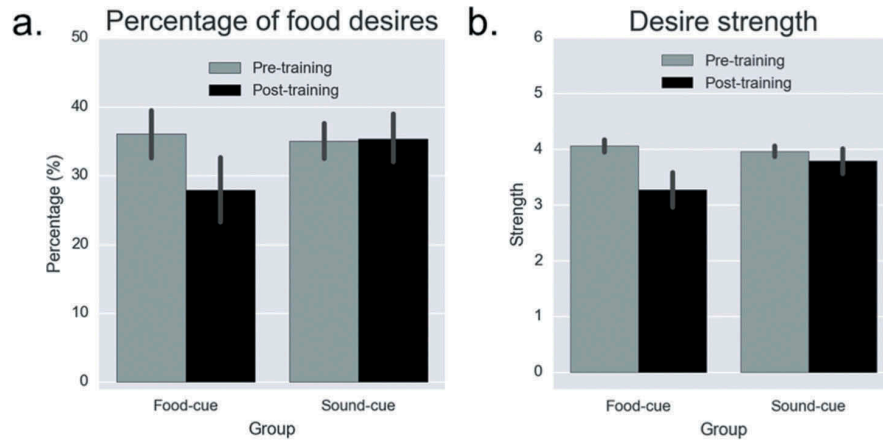


Figure 2. EMA sampling revealed a reduction in (a) percentage of food desires and (b) average desire strength following food-cue but not sound-cue training. Error bars indicate S.E.M.

cues in the VS, $t(34) = 1.4$, $p = 0.18$, $d = 0.45$, or the OFC, $t(34) = 1.7$, $p = 0.10$, $d = 0.56$. A significant training group by time interaction was observed following training in both regions (VS: $F(1, 34) = 8.1$, $p = 0.007$, $\eta_p^2 = 0.19$; OFC: $F(1, 34) = 4.0$, $p = 0.05$, $\eta_p^2 = 0.10$). Following training, the food-cue training group showed a significant reduction in both VS (pre-training: $M = 0.12$; post-training: $M = -0.02$, $t(17) = 2.5$, $p = 0.02$, $d = 0.75$; Figure 3a) and OFC (pre-training: $M = 0.40$; post-training: $M = 0.03$, $t(17) = 3.8$, $p = 0.001$, $d = 1.28$; Figure 3b) ROIs, but the sound-cue training group showed no significant reduction in the VS (pre-training: $M = 0.05$; post-training: $M = 0.11$, $t(17) = -1.4$, $p = 0.18$, $d = -0.42$; Figure 3a) and OFC (pre-training: $M = 0.24$; post-training: $M = 0.11$, $t(17) = 1.8$, $p = 0.09$, $d = 0.52$; Figure 3b).

Neuroimaging results: training effect on reward and control system activity

Before training, the food – and sound cue – training groups did not differ in brain responsivity to food cues in the reward system, $t(34) = 0.9$, $p = 0.35$, $d = 0.31$ (Figure 4a). A significant training group by time interaction was observed following training (group \times time interaction, $F(1, 34) = 5.4$, $p = 0.02$, $\eta_p^2 = 0.13$) (Figure 4a). Following training, the food-cue training group showed a significant reduction in reward system activity (pre-training: $M = 0.08$; post-training: $M = -0.002$; $t(17) = -2.2$, $p = 0.04$, $d = -0.71$), whereas the sound-cue training group showed no change (pre-training: $M = 0.05$; post-training: $M = 0.09$; $t(17) = 1.0$, $p = 0.29$, $d = 0.37$).

In the FP control system, the two groups showed no difference in responsivity to food cues before training, $t(34) = -0.19$, $p = 0.35$, $d = -0.06$ (Figure 4b). After training,

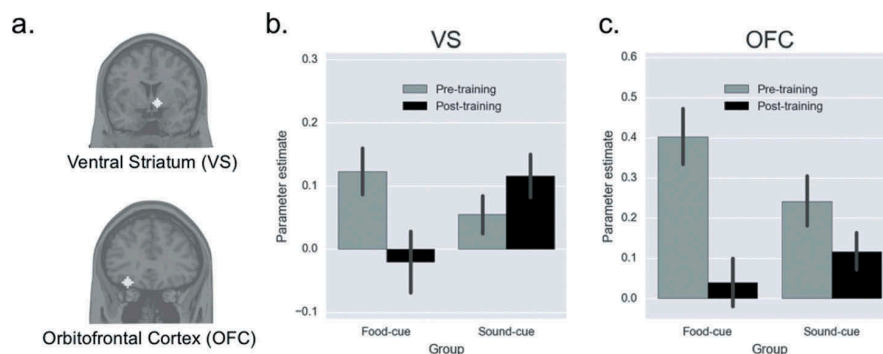


Figure 3. Food-cue training reduces reward activity to food cues in VS and OFC. The location of the right VS and left OFC ROIs were indicated (a). ROI analyses show food-cue reactivity in the right VS (b) and the left OFC (c) before and after food – or sound-cue stop signal training. Both regions demonstrated a significant training group by time interaction such that the food-cue training group showed a significant reduction in activity following training whereas the sound-cue training group did not. Error bars indicate S.E.M.

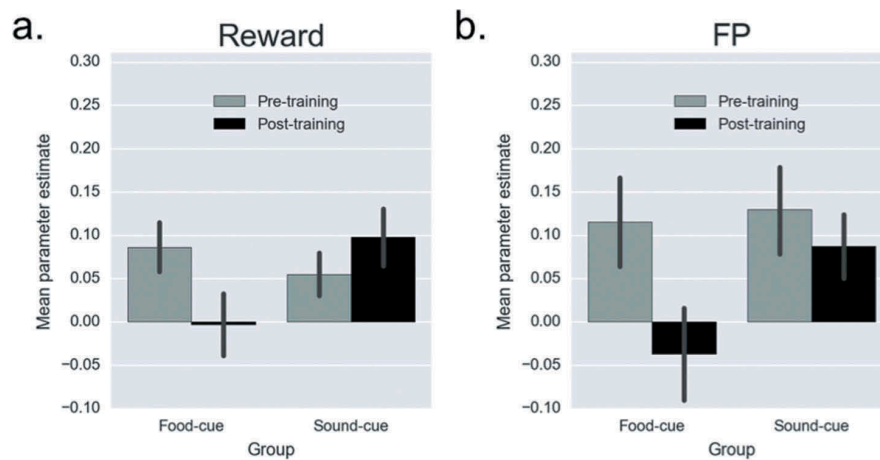


Figure 4. Food-cue training reduces overall reactivity in both reward and frontoparietal (FP) control systems. System-wide activity for the reward system (a) and the FP control system (b) is shown before and after food – or sound-cue stop signal training. The food-cue training group showed a significant reduction in overall reward system activity and a marginal reduction in overall FP control system activity following training. Error bars indicate S.E.M.

the food-cue training group revealed a reduction trend in the FP control system (pre-training: $M = 0.11$; post-training: $M = -0.03$; $t(17) = -1.7$, $p = 0.09$, $d = -0.68$), whereas the sound-cue training group showed no significant change (pre-training: $M = 0.12$; post-training: $M = 0.08$; $t(17) = -0.6$, $p = 0.53$, $d = -0.22$); group \times time interaction, $F(1, 34) = 1.0$, $p = 0.32$, $\eta_p^2 = 0.02$ (Figure 4b). Of particular importance, the reductions observed in the FP control system following food-cue training were significantly correlated with reduced activity within the reward system ($r = 0.61$, $p = 0.006$; Figure 5).

Discussion

Domain-specific food-cue inhibitory training successfully reduced food cue-responsivity in VS and left OFC, as well as everyday eating desires, whereas domain-general sound-cue inhibitory training showed no such reduction after two weeks of training. Thus, although our hypothesis that self-regulation training would reduce brain reward responsivity and everyday eating desires was supported, this finding obtained only for the domain-specific training group. The ineffectiveness of sound-cue inhibitory training suggests that self-regulatory training may be more effective when inhibitory training paradigms are tailored to the to-be-resisted cue. Collectively, these behavioral and neuroimaging findings do not support the idea that domain-general inhibitory training can strengthen self-regulatory resources. We consider each in turn.

As previously demonstrated in numerous studies, training on the inhibitory tasks produces practice effects, such that people get better inhibiting behavior

over time (Beauchamp, Kahn, & Berkman, 2016; Berkman et al., 2014). In our study, both the domain-general sound-cue training group and the domain-specific food-cue training group showed robust increases in SST performance with training. However, we found that domain-specific food-cue training was more effective in reducing daily food desires than was domain-general sound-cue training. This pattern is in keeping with the emerging literature demonstrating limited cross-domain transfer of training (Beauchamp et al., 2016; Melby-Lervåg & Hulme, 2013; Melby-Lervåg et al., 2016; Owen et al., 2010; Veling et al., 2011).

In addition to reducing food cravings in daily life, the domain-specific training task also reduced reward activity to appetitive food cues in the brain regions related to reward processing, including the VS and OFC. The VS and OFC have been consistently found to represent reward value and motivational salience of appetitive food stimuli (Demos et al., 2012; Demos, Kelley, & Heatherton, 2011; Kringelbach, O'Doherty, Rolls, & Andrews, 2003; Lopez et al., 2014; O'Doherty, Rolls, Francis, Bowtell, & McGlone, 2001; Passamonti et al., 2009; Stoeckel et al., 2008; Wagner et al., 2013, 2012; Wang et al., 2004). In neuroimaging studies, the strength of OFC responsivity to food cues is linked to subjective reports of liking of food items (O'Doherty et al., 2001; Wagner et al., 2013), and desire for food (Wang et al., 2009). Heightened VS activity is also associated with a tendency to overeat (Demos et al., 2011; Lopez et al., 2014) and even predicts long-term weight gains (Demos et al., 2012). Furthermore, those with self-regulatory problems related to overeating (e.g. obese individuals) also show heightened food-cue responsivity in the VS and OFC (Carnell, Gibson, Benson, Ochner, & Geliebter,

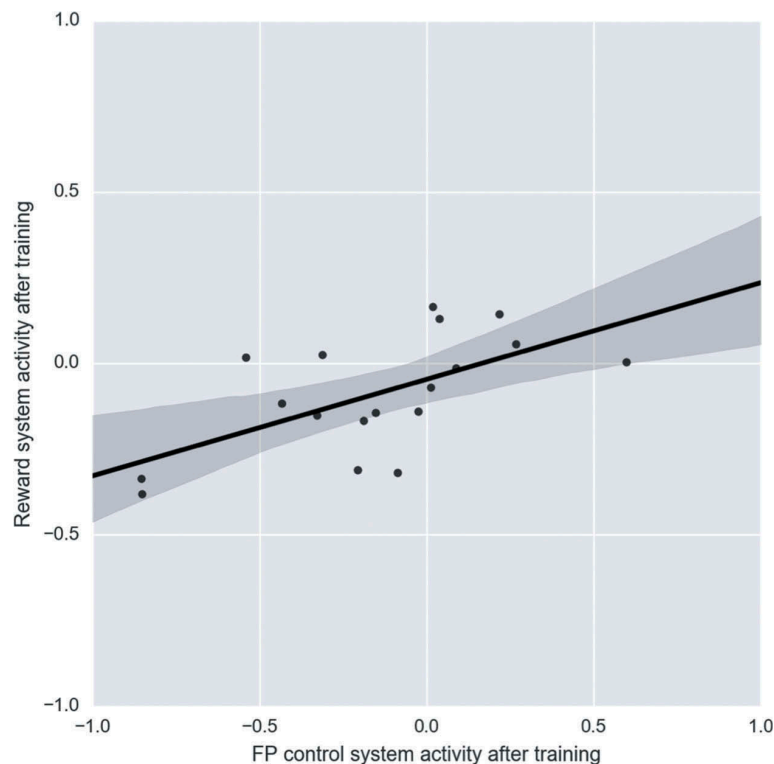


Figure 5. Food-cue training reductions in FP control system activity are correlated with post-training reductions in reward system activity. Signal change reflects pre-training versus post-training differences in the reward system (y-axis) and FP control system (x-axis). Negative values indicate reduced activity following training.

2011; Rapuano, Huckins, Sargent, Heatherton, & Kelley, 2015; Stoeckel et al., 2009). Indeed, in our study, depleted dieters in both training groups exhibited exaggerated responses to food cues in the VS and OFC before the training. Together, these findings suggest that heightened food-cue responsivity in reward regions may be an indicator of self-regulatory failures in dieting (Demos et al., 2012, 2011; Heatherton & Wagner, 2011; Kelley, Wagner, & Heatherton, 2015). It follows that effective self-regulatory training strategies may function to lower brain responsivity to appetitive food cues in these reward regions. In addition, the OFC plays a crucial role in contingency-based reinforcement, which means that it codes the expected values of the stimulus (Levy & Glimcher, 2012; Li, Vanni-Mercier, Isnard, Mauguier, & Dreher, 2016; Padoa-Schioppa & Cai, 2011). Lower OFC responses to stimulus cues may signal lower expected values of the same stimulus after the food-cue inhibitory training. These lower OFC responses may then mediate the inhibitory mechanisms by updating signals to inform the brain control systems that less exertion of inhibitory efforts is needed after training.

This possibility is supported from our findings in the frontoparietal (FP) control system. In contrast to the training-related reductions in reward responsivity

following food-inhibition training, we did not observe commensurate *increases* in activity in brain regions typically associated with cognitive control following either training program. Rather, we found that food-cue specific inhibitory training reduced activity in regions of the FP control system, including the IFG, the superior frontal gyrus, and the inferior parietal lobule. Although this finding seems contradictory to the proposition of the strength model, which is that self-regulation can be enhanced through strengthening inhibitory control (Baumeister et al., 1998), a recent review suggests another possibility. Kelley et al. (2015) noted that both increased and decreased brain activity in the FP system has been interpreted as self-regulatory success, with some studies arguing that heightened brain activity may represent increased self-regulatory strength, and others interpreting control system increases as reflecting more effortful but inefficient self-regulatory attempts. In fact, this latter interpretation fits nicely with the Excessive Recruitment Model, in that the heightened activity in the FP system was a maladaptive self-regulatory indicator, especially in long-term self-regulatory behaviors (Chester et al., 2016).

One interpretation of the decreased activity in the FP system, then, is that individuals engaged in more efficient, less effortful self-regulation following food-cue training. This possibility is supported by other self-regulatory training studies. In one short-term training study (Schonberg, Bakkour, Hover, Mumford, & Poldrack, 2013), participants were trained with monetary incentives to select a less preferred food item over a more preferred one. In early trials, this selection activated the LPFC. Following practice, however, the LPFC showed decreased activity. A similar pattern was reported by Berkman and colleagues (Berkman et al., 2014). After two weeks of training on the stop-signal task, neural activity in fronto-parietal brain regions decreased during the inhibition implementation period. Findings from these two studies and the present one favor the idea that decreased activity in the FP system may be a marker of efficient, but less effortful, attempts during self-regulation, especially with repeated practice. Put simply, individuals improve their self-regulation for the tasks they practice, but these practice effects do not appear to generalize to other, non-practiced self-regulation tasks. Such findings complement a broad neuroimaging literature on skill learning (Dayan & Cohen, 2011; Petersen, Van Mier, Fiez, & Raichle, 1998). With practice, neural activity in brain regions that engage in a particular skill lessens as the skill becomes automatic. It is plausible that after two weeks of food-cue inhibitory training, dieters become more proficient in regulating their food desires and doing so become less conscious and effortful and more automatic. This account receives further support from the finding that FP and reward system decreases following food-cue training were correlated; dieters with stronger FP reductions showed commensurate reductions in the reward system.

Methodological and conceptual limitations

Although the current study presents initial evidence supporting a relationship between domain-specific training and self-regulation success, several limitations warrant caution in interpreting these findings. First, the current study lacks an additional control group to rule out the possibility that the reduction in food desire was due to the habituation effect of exposure to appetitive food images rather than the inhibitory training effect on food cues. Although our current findings cannot rule out this possibility, Lawrence and colleagues (Lawrence et al., 2015a; Lawrence, Verbruggen, Morrison, Adams, & Chambers, 2015b) conducted two behavioral studies and found that compared to individuals who received

inhibition training to food images, those who received merely exposure training not only consumed more food (Lawrence et al., 2015b), but also gained weight after two-weeks of training (Lawrence et al., 2015a). This suggests that mere exposure to food cues is unlikely to produce alterations in brain activity as we observed in our study. The available evidence therefore suggests that inhibitory training is a critical ingredient for bolstering self-regulation. Of course, future studies are needed to verify this proposition as well as to rule out the potential effect of habituation on brain reward activity.

Second, there are additional differences between the domain-specific and domain-general training tasks and their relation to real-world self-regulation. Whereas the domain-specific-training task uses visual food cues as the “stop signal”, the domain-general training task uses auditory tones as the “stop signal”. This was sensory modality switch was purposeful, as it provided an opportunity to contrast a more domain-specific training task with what has been considered the gold-standard stop signal training task used in the literature to date. However, the modality switch leaves open the possibility that the effects on eating behavior could have been driven by the modality switch (i.e. inhibiting to any visual cue produces domain-general training, whereas auditory stop signals do not). Although this possibility cannot be specifically ruled out when considering the present study in isolation, several studies have reported that domain-general training using nonspecific visual cues have minimal transfer effects (Beauchamp et al., 2016; Berkman et al., 2014). More generally, the domain-specific training task (inhibiting a button press when a food image appears) is also not perfectly matched to the kind of self-regulatory behaviors that dieters experience in the real world (e.g. resisting eating a cheeseburger when driving past a fast food restaurant at lunch).

The present study uses the term “domain-specific” to simply mean that practicing inhibitory control may benefit when the cue is an actual reward cue that is relevant to real-world self-regulation. One speculation then is that any appetizing, food-related cue that would provoke craving in the real world (e.g. the smell of chocolate chip cookies, a taste of a chocolate shake, or the sound of bacon sizzling) would serve as a suitable “stop” signal (albeit some of the cues would be more difficult to implement in the context of a neuroimaging paradigm). Our initial findings suggest that inhibitory training may hold value for improving self-regulation when stop signals are behaviorally relevant. Future work is needed to explore the extent to which other domain-relevant cues may allow for even better outcomes.

A third potential problem with the food-cue inhibitory task is that it potentially creates demand characteristics for the EMA surveys, as participants assigned to this condition might respond differently to the surveys because they were aware that the goal of the training was to help reduce food cravings in daily life. Two factors argue against this potential confound. First, all of the participants were enrolled because they were interested in regulating their eating behavior. Second, all of the dieters enrolled in the study were told that the training was intended to improve self-regulation (i.e. the participants were naïve to the domain-specific/domain-general study design and all participants believed that the training was intended to help them improve self-regulation).

Finally, the sample size reported here is necessarily small given the costs of multiple scanning sessions and high training demands. In addition, since the exclusive recruitment of female dieters may prevent the confounding effect from gender difference (Pingitore, Spring, & Garfield, 1997), future studies need to examine the generalization effect in the food-cue inhibitory training for both genders. Future work is also needed to replicate these initial results in other dieting populations with both genders and to extend these findings to other appetitive behaviors (e.g. nicotine and alcohol use) that may benefit from domain-specific training programs.

Implications and future directions

Taken together our findings highlight a paradoxical issue in self-regulation, namely – depletion disrupts self-regulation in a domain general fashion, whereas training may necessarily require domain-specific training to be truly effective. Our findings suggest that a revised strength model of self-regulation is needed to explain this paradox. Myriad studies have shown that depletion in one domain can lead to self-regulation failure in other domains. For example, following an effortful working memory task, individuals had more difficulty inhibiting high reward-anticipation cues than low reward-anticipation cues in a motor inhibition task (Freeman & Aron, 2016). Similar patterns are also found in other domains: suppressing emotion can lead to subsequent binge eating behaviors (Vohs & Heatherton, 2000), and engaging in an effortful thought suppression task can result in increased impulsivity during interpersonal interactions (Vohs et al., 2005). By contrast, there is little evidence to support the idea that self-regulation can be strengthened through domain-general training (Beauchamp et al., 2016; Berkman et al., 2014). Rather than

strengthening the overall capacity of a domain general self-regulation resource, repeated training of an inhibitory task may reduce the overall effort needed to perform the specific training task, a notion that is consistent with a broad literature on procedural learning (Dayan & Cohen, 2011; Petersen et al., 1998). In this way, food temptations are not being overcome by stronger inhibition, they are simply easier to suppress through practice.

Indeed, this notion may help explain the behavioral pattern observed during EMA sampling. Following food-inhibition training, subjects reported fewer and weaker food desires in their daily lives. These findings fit nicely with the practice effects suggested here as we believe our domain-specific inhibitory task specifically target desire. An open question is whether other domain-general or domain-specific approaches that focus on inhibiting enactment more directly than desire (e.g. meditation, mindfulness) may be similarly efficacious. For example, mindfulness interventions do not require active inhibition of food desires, instead focusing on acknowledging the automatic, reward-related response and subsequently inhibiting enactment (Brewer et al., 2011; Tang, Posner, Rothbart, & Volkow, 2015; Tang, Tang, & Posner, 2013; Westbrook et al., 2013). Similarly, cognitive reappraisal strategies focus on changing or shaping reward-related responses after they occur (Giuliani, Mann, Tomiyama, & Berkman, 2014; Kober et al., 2010). Behaviorally, such approaches have proven effective in reducing cravings in smokers controlling cravings towards palatable foods, perhaps because inhibiting the fast, automatic reward responses to learned cues may be more taxing to inhibit than a more deliberate, conscious decision to act on reward signals.

One interesting implication of the present finding is that if self-regulation is a limited resource, then training within a domain may free up self-regulatory resources for other domains. If dieters exert much of their self-regulatory effort controlling food intake, it may leave them with minimal resources to deal with other behavioral or emotional needs (Baumeister & Heatherton, 1996). To the extent that training makes it easier to inhibit food desires, this frees up self-regulatory resources to deal with daily life stressors. The key point here is that such training must be relevant to real world behavior. Learning to inhibit motor responses to auditory tones may produce effortless inhibitory skills that are never called upon – the absence of any need in the real world to inhibit to auditory tones means that becoming good at it does not free up any self-regulatory resources for situations that require inhibition.

An exciting new aspect of our findings is the potential for mobilization of training programs onto smartphone and tablet platforms. To the extent that both training and assessment of appetitive behavior and self-regulatory outcomes can be administered and measured in real-world settings, future work may benefit from larger scale behavioral studies across thousands of participants in ways that cannot be accomplished in a laboratory setting.

Acknowledgments

We are grateful to Wilhelm Hofmann, Melina Gehring and Elizabeth Tremmel for comments on the manuscript. We also thank Ying Lin and Mary D'Geronimo for help with data collection. This work was supported by a grant from the National Institutes of Health (R01DA022582). The authors declare no competing financial interests.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was supported by the National Institutes of Health [R01DA022582];

ORCID

Pin-Hao A. Chen  <http://orcid.org/0000-0002-6791-526X>

References

- Baumeister, R. F., Bratslavsky, E., Muraven, M., & Tice, D. M. (1998). Ego depletion: Is the active self a limited resource? *Journal of Personality and Social Psychology*, 74(5), 1252–1265.
- Baumeister, R. F., & Heatherton, T. F. (1996). Self-regulation failure: An overview. *Psychological Inquiry*, 7(1), 1–15.
- Baumeister, R. F., Vohs, K. D., & Tice, D. M. (2007). The strength model of self-control. *Current Directions in Psychological Science*, 16(6), 351–355.
- Beauchamp, K. G., Kahn, L. E., & Berkman, E. T. (2016). Does inhibitory control training transfer?: Behavioral and neural effects on an untrained emotion regulation task. *Social Cognitive and Affective Neuroscience*, nsw061. <http://doi.org/10.1093/scan/nsw061>
- Berkman, E. T., Graham, A. M., & Fisher, P. A. (2012). Training self-control: A domain-general translational neuroscience approach. *Child Development Perspectives*, 6(4), 374–384. <http://doi.org/10.1111/j.1750-8606.2012.00248.x>
- Berkman, E. T., Kahn, L. E., & Merchant, J. S. (2014). Training-induced changes in inhibitory control network activity. *Journal of Neuroscience*, 34(1), 149–157.
- Bertrams, A., & Schmeichel, B. J. (2013). Improving self-control by practicing logical reasoning. *Self and Identity*, 13(4), 419–431. <http://doi.org/10.1080/15298868.2013.836562>
- Blechert, J., Meule, A., Busch, N. A., & Ohla, K. (2014). Food-pics: An image database for experimental research on eating and appetite. *Frontiers in Psychology*, 5(617), 1–10.
- Brewer, J. A., Mallik, S., Babuscio, T. A., Nich, C., Johnson, H. E., Deleone, C. M., Minnick-Cotton, C. A., ... Rounsaville, B. J. (2011). Mindfulness training for smoking cessation: Results from a randomized controlled trial. *Drug and Alcohol Dependence*, 119(1–2), 72–80. <http://doi.org/10.1016/j.drugalcdep.2011.05.027>
- Carnell, S., Gibson, C., Benson, L., Ochner, C. N., & Geliebter, A. (2011). Neuroimaging and obesity: Current knowledge and future directions. *Obesity Reviews*, 13(1), 43–56. <http://doi.org/10.1111/j.1467-789X.2011.00927.x>
- Chen, P.-H. A., Chavez, R. S., & Heatherton, T. F. (2017). Structural integrity between executive control and reward regions of the brain predicts body fat percentage in chronic dieters. *Cognitive Neuroscience*, 8(3), 162–166. <http://doi.org/10.1080/17588928.2016.1235556>
- Chester, D. S., Lynam, D. R., Milich, R., Powell, D. K., Andersen, A. H., & DeWall, C. N. (2016). How do negative emotions impair self-control? A neural model of negative urgency. *NeuroImage*, 132, 43–50.
- Collaboration, O. S. (2015). Estimating the reproducibility of psychological science. *Science*, 349(6251), 4716. <http://doi.org/10.1126/science.aac4716>
- Dayan, E., & Cohen, L. G. (2011). Neuroplasticity subserving motor skill learning. *Neuron*, 72(3), 443–454.
- Demos, K. E., Heatherton, T. F., & Kelley, W. M. (2012). Individual differences in nucleus accumbens activity to food and sexual images predict weight gain and sexual behavior. *Journal of Neuroscience*, 32(16), 5549–5552.
- Demos, K. E., Kelley, W. M., & Heatherton, T. F. (2011). Dietary restraint violations influence reward responses in nucleus accumbens and amygdala. *Journal of Cognitive Neuroscience*, 23(8), 1952–1963.
- Dosenbach, N. U. F., Fair, D. A., Miezin, F. M., Cohen, A. L., Wenger, K. K., Dosenbach, R. A. T., et al. (2007). Distinct brain networks for adaptive and stable task control in humans. *Proceedings of the National Academy of Sciences*, 104(26), 11073–11078.
- Finkel, E. J., DeWall, C. N., Slotter, E. B., Oaten, M., & Foshee, V. A. (2009). Self-regulatory failure and intimate partner violence perpetration. *Journal of Personality and Social Psychology*, 97(3), 483–499.
- Freeman, S. M., & Aron, A. R. (2016). Withholding a reward-driven action: Studies of the rise and fall of motor activation and the effect of cognitive depletion. *Journal of Cognitive Neuroscience*, 28(2), 237–251.
- Gailliot, M. T., Plant, E. A., Butz, D. A., & Baumeister, R. F. (2007). Increasing self-regulatory strength can reduce the depleting effect of suppressing stereotypes. *Personality and Social Psychology Bulletin*, 33(2), 281–294.
- Giuliani, N. R., Mann, T., Tomiyama, A. J., & Berkman, E. T. (2014). Neural systems underlying the reappraisal of personally craved foods. *Journal of Cognitive Neuroscience*, 26(7), 1390–1402.
- Hagger, M. S., Wood, C., Stiff, C., & Chatzisarantis, N. L. D. (2010). Ego depletion and the strength model of self-control: A meta-analysis. *Psychological Bulletin*, 136(4), 495–525. <http://doi.org/10.1037/a0019486>
- Heatherton, T. F., Herman, C. P., Polivy, J., King, G. A., & McGree, S. T. (1988). The (mis)measurement of restraint:

- An analysis of conceptual and psychometric issues. *Journal of Abnormal Psychology*, 97(1), 19–28.
- Heatherton, T. F., Polivy, J., & Herman, C. P. (1991). Restraint, weight loss, and variability of body weight. *Journal of Abnormal Psychology*, 100(1), 78–83.
- Heatherton, T. F., & Wagner, D. D. (2011). Cognitive neuroscience of self-regulation failure. *Trends in Cognitive Sciences*, 15(3), 132–139.
- Hofmann, W., & Patel, P. V. (2015). SurveySignal: A convenient solution for experience sampling research using participants' own smartphones. *Social Science Computer Review*, 33(2), 235–253.
- Huckins, J., Adeyemo, B., Miezin, F. M., Power, J. D., Gordon, E. M., Laumann, T. O., ... Kelley, W. M. (2018). Reward-related regions form a preferentially coupled system at rest. *bioRxiv*, 304865. <http://doi.org/10.1101/304865>
- Hui, S.-K. A., Wright, R. A., Stewart, C. C., Simmons, A., Eaton, B., & Nolte, R. N. (2009). Performance, cardiovascular, and health behavior effects of an inhibitory strength training intervention. *Motivation and Emotion*, 33(4), 419–434. <http://doi.org/10.1007/s11031-009-9146-0>
- Kelley, W. M., Wagner, D. D., & Heatherton, T. F. (2015). In search of a human self-regulation system. *Annual Review of Neuroscience*, 38(1), 389–411.
- Kober, H., Mende-Siedlecki, P., Kross, E. F., Weber, J., Walter Mischel, C. L., Hart, E. F., & Ochsner, K. N. (2010). Prefrontal–Striatal pathway underlies cognitive regulation of craving. *Proceedings of the National Academy of Sciences*, 107, 14811–14816. <http://doi.org/10.1073/pnas.1007791107/-DCSupplemental>
- Kringelbach, M. L., O'Doherty, J., Rolls, E. T., & Andrews, C. (2003). Activation of the human orbitofrontal cortex to a liquid food stimulus is correlated with its subjective pleasantness. *Cerebral Cortex*, 13, 1064–1071.
- Lawrence, N. S., O'Sullivan, J., Parslow, D., Javaid, M., Adams, R. C., Chambers, C. D., ... Verbruggen, F. (2015a). Training response inhibition to food is associated with weight loss and reduced energy intake. *Appetite*, 95, 17–28. <http://doi.org/10.1016/j.appet.2015.06.009>
- Lawrence, N. S., Verbruggen, F., Morrison, S., Adams, R. C., & Chambers, C. D. (2015b). Stopping to food can reduce intake. Effects of stimulus-specificity and individual differences in dietary restraint. *Appetite*, 85, 91–103.
- Levy, D. J., & Glimcher, P. W. (2012). The root of all value: A neural common currency for choice. *Current Opinion in Neurobiology*, 22(6), 1027–1038.
- Li, Y., Vanni-Mercier, G., Isnard, J., Mauguier, F., & Dreher, J.-C. (2016). The neural dynamics of reward value and risk coding in the human orbitofrontal cortex. *Brain*, 139(Pt 4), 1295–1309. <http://doi.org/10.1093/brain/awv409>
- Lopez, R. B., Chen, P.-H. A., Huckins, J. F., Hofmann, W., Kelley, W. M., & Heatherton, T. F. (2017). A balance of activity in brain control and reward systems predicts self-regulatory outcomes. *Social Cognitive and Affective Neuroscience*. <http://doi.org/10.1093/scan/nsx004>
- Lopez, R. B., Hofmann, W., Wagner, D. D., Kelley, W. M., & Heatherton, T. F. (2014). Neural predictors of giving in to temptation in daily life. *Psychological Science*, 25(7), 1337–1344.
- Melby-Lervåg, M., & Hulme, C. (2013). Is working memory training effective? A meta-analytic review. *Developmental Psychology*, 49(2), 270–291.
- Melby-Lervåg, M., Redick, T. S., & Hulme, C. (2016). Working memory training does not improve performance on measures of intelligence or other measures of “far transfer”: Evidence from a meta-analytic review. *Perspectives on Psychological Science: a Journal of the Association for Psychological Science*, 11(4), 512–534.
- Muraven, M. (2010). Building self-control strength: Practicing self-control leads to improved self-control performance. *Journal of Experimental Social Psychology*, 46(2), 465–468.
- Muraven, M., Baumeister, R. F., & Tice, D. M. (1999). Longitudinal improvement of self-regulation through practice: Building self-control strength through repeated exercise. *The Journal of Social Psychology*, 139(4), 446–457.
- O'Doherty, J. P., Rolls, E. T., Francis, S., Bowtell, R., & McGlone, F. (2001). Representation of pleasant and aversive taste in the human brain. *Journal of Neurophysiology*, 85(3), 1315–1321.
- Owen, A. M., Hampshire, A., Grahn, J. A., Stenton, R., Dajani, S., Burns, A. S., et al. (2010). Putting brain training to the test. *Nature*, 465(7299), 775–778. <http://doi.org/10.1038/nature09042>
- Padoa-Schioppa, C., & Cai, X. (2011). The orbitofrontal cortex and the computation of subjective value: Consolidated concepts and new perspectives. *Annals of the New York Academy of Sciences*, 1239(1), 130–137.
- Passamonti, L., Rowe, J. B., Schwarzbauer, C., Ewbank, M. P., Hagen, Von Dem, E., & Calder, A. J. (2009). Personality predicts the brain's response to viewing appetizing foods: The neural basis of a risk factor for overeating. *Journal of Neuroscience*, 29(1), 43–51. <http://doi.org/10.1523/JNEUROSCI.4966-08.2009>
- Petersen, S. E., & Posner, M. I. (2012). The attention system of the human brain: 20 years after. *Annual Review of Neuroscience*, 35(1), 73–89.
- Petersen, S. E., & Sporns, O. (2015). Brain networks and cognitive architectures. *Neuron*, 88(1), 207–219.
- Petersen, S. E., Van Mier, H., Fiez, J. A., & Raichle, M. E. (1998). The effects of practice on the functional anatomy of task performance. *Proceedings of the National Academy of Sciences of the United States of America*, 95(3), 853–860.
- Pingitore, R., Spring, B., & Garfield, D. (1997). Gender differences in body satisfaction. *Obesity Research*, 5(5), 402–409.
- Power, J. D., Cohen, A. L., Nelson, S. M., Wig, G. S., Barnes, K. A., Church, J. A., ... Petersen, S. E. (2011). Functional network organization of the human brain. *Neuron*, 72(4), 665–678. <http://doi.org/10.1016/j.neuron.2011.09.006>
- Rapaport, K. M., Huckins, J. F., Sargent, J. D., Heatherton, T. F., & Kelley, W. M. (2015). Individual Differences in Reward and Somatosensory-Motor Brain Regions Correlate with Adiposity in Adolescents, Cerebral Cortex. bhv097. <http://doi.org/10.1093/cercor/bhv097>
- Schonberg, T., Bakkour, A., Hover, A. M., Mumford, J. A., & Poldrack, R. A. (2013). Influencing food choices by training: Evidence for modulation of frontoparietal control signals. *Journal of Cognitive Neuroscience*, 1–22. <http://doi.org/10.1111/j.1460-9568.2004.03095.x>
- Stoeckel, L. E., Kim, J., Weller, R. E., Cox, J. E., Cook, E. W., & Horwitz, B. (2009). Effective connectivity of a reward network in obese women. *Brain Research Bulletin*, 79(6), 388–395.
- Stoeckel, L. E., Weller, R. E., Cook, E. W., III, Twieg, D. B., Knowlton, R. C., & Cox, J. E. (2008). Widespread reward-

- system activation in obese women in response to pictures of high-calorie foods. *NeuroImage*, 41(2), 636–647.
- Tang, Posner, M. I., Rothbart, M. K., & Volkow, N. D. (2015). Circuitry of self-control and its role in reducing addiction. *Trends in Cognitive Sciences*, 19(8), 439–444. <http://doi.org/10.1016/j.tics.2015.06.007>
- Tang, Tang, R., & Posner, M. I. (2013). Brief meditation training induces smoking reduction. *Proceedings of the National Academy of Sciences*, 110(34), 13971–13975. <http://doi.org/10.1073/pnas.1311887110>
- Veling, H., Aarts, H., & Papies, E. K. (2011). Using stop signals to inhibit chronic dieters' responses toward palatable foods. *Behaviour Research and Therapy*, 49(11), 771–780.
- Veling, H., Aarts, H., & Stroebe, W. (2013). Using stop signals to reduce impulsive choices for palatable unhealthy foods. *British Journal of Health Psychology*, 18(2), 354–368.
- Verbruggen, F., & Logan, G. D. (2008). Response inhibition in the stop-signal paradigm. *Trends in Cognitive Sciences*, 12(11), 418–424.
- Vohs, K. D., Baumeister, R. F., & Ciarocco, N. J. (2005). Self-regulation and self-presentation: Regulatory resource depletion impairs impression management and effortful self-presentation depletes regulatory resources. *Journal of Personality and Social Psychology*, 88(4), 632–657.
- Vohs, K. D., & Heatherton, T. F. (2000). Self-regulatory failure: A resource-depletion approach. *Psychological Science*, 11(3), 249–254.
- Wagner, D. D., Altman, M., Boswell, R. G., Kelley, W. M., & Heatherton, T. F. (2013). Self-regulatory depletion enhances neural responses to rewards and impairs top-down control. *Psychological Science*, 24(11), 2262–2271.
- Wagner, D. D., Boswell, R. G., Kelley, W. M., & Heatherton, T. F. (2012). Inducing negative affect increases the reward value of appetizing foods in dieters. *Journal of Cognitive Neuroscience*, 24(7), 1625–1633.
- Wagner, D. D., & Heatherton, T. F. (2012). Self-regulatory depletion increases emotional reactivity in the amygdala. *Social Cognitive and Affective Neuroscience*, 8, 410–417. <http://doi.org/10.1093/scan/nss082>
- Wagner, D. D., & Heatherton, T. F. (2015). Self-regulation and its failure: The seven deadly threats to self-regulation. In *APA handbook of personality and social psychology, Volume 1: Attitudes and social cognition*. (pp. 805–842). Washington: American Psychological Association. <http://doi.org/10.1037/14341-026>
- Wang, G.-J., Volkow, N. D., Telang, F., Jayne, M., Ma, J., Rao, M., Zhu, W., ... Fowler, J. S. (2004). Exposure to appetitive food stimuli markedly activates the human brain. *NeuroImage*, 21(4), 1790–1797. <http://doi.org/10.1016/j.neuroimage.2003.11.026>
- Wang, G.-J., Volkow, N. D., Telang, F., Jayne, M., Ma, Y., Pradhan, K., et al. (2009). Evidence of gender differences in the ability to inhibit brain activation elicited by food stimulation. *Proceedings of the National Academy of Sciences of the United States of America*, 106(4), 1249–1254.
- Westbrook, C., Creswell, J. D., Tabibnia, G., Julson, E., Kober, H., & Tindle, H. A. (2013). Mindful attention reduces neural and self-reported cue-induced craving in smokers. *Social Cognitive and Affective Neuroscience*, 8(1), 73–84.