

What Can Cognitive Neuroscience Tell Us About the Mechanism of Ego Depletion?

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The last decade has seen an ever-increasing interest in using the tools and methods of cognitive neuroscience to examine the brain systems involved in self-regulation and its failure (Heatherton & Wagner, 2011). Although the study of related topics, such as cognitive control, response inhibition, and the executive functions, have long been mainstays of cognitive neuroscience, research on self-regulation and self-regulation failure is a more recent phenomenon. Findings from this work have not only helped specify the brain mechanisms that underlie successful self-regulation, but they have also resulted in new ways of thinking about self-control and the reasons why it sometimes breaks down. Indeed, it is already the case that research findings from cognitive neuroscience are whittling their way back into psychological theory as evidenced by the increasing use of neuroscientific research in contemporary theories of self-regulation (Denson, DeWall, & Finkel, 2012; Hofmann, Schmeichel, & Baddeley, 2012; Inzlicht, Elkins-Brown, & Berkman, 2015; Inzlicht, Legault, & Teper, 2014; Inzlicht, Schmeichel, & Macrae, 2014; Kelley, Wagner, & Heatherton, 2015, Chapter 13).

As prior research has consistently shown, the ability to self-regulate is impaired following prior bouts of effortful self-control (Baumeister, Bratslavsky, Muraven, & Tice, 1998; Vohs & Heatherton, 2000; for a meta-analysis see Hagger, Wood, Stiff, & Chatzisarantis, 2010). However, there remains much debate concerning the mechanism for this

phenomenon (Inzlicht & Berkman, 2015; Inzlicht & Schmeichel, 2012; Inzlicht, Schmeichel, & Macrae, 2014; Job, Dweck, & Walton, 2010, Chapter 11, Chapter 20). In this chapter, we review findings from cognitive neuroscience on the brain systems involved in ego depletion and how these may inform discussions of the mechanisms of ego depletion. We begin our chapter by first presenting an overview of several cognitive neuroscience methods and how they might be applied to the study of self-regulation failure and ego depletion. We then examine the extant neuroscience research on ego depletion, looking at how brain systems involved in self-control and reward processing are affected by ego depletion. Finally, we review recent neuroscience informed models of ego depletion that seek either to challenge or extend the limited resource model of self-regulation.

BRIEF OVERVIEW OF COGNITIVE NEUROSCIENCE METHODS

There are many tools in the cognitive neuroscience toolbox that have been used to study self-regulation and related topics. These tools can be grouped into three categories: those based on measuring or perturbing the electrical activity of the brain [eg, electroencephalography (EEG), magnetoencephalography (MEG), transcranial magnetic stimulation (TMS)], those based on detecting regional changes in blood flow (PET, fMRI) and those designed to assess anatomy and anatomical connectivity (MRI, DTI). In general, there is a trade-off between spatial and temporal resolution, such that measures of electrical activity are ideal for detecting the temporal dynamics of psychological processes but are comparatively poor at determining the precise location. Conversely, measures based on detecting blood flow changes are optimized for locating activity in the brain but suffer from poor temporal resolution. In this section, we give a brief overview of several of these methods, along with examples of how they have been, or may be, used to study ego depletion.

Electroencephalography and Magnetoencephalography

EEG is a method aimed at directly measuring the electrical potentials generated by ongoing neural activity with a temporal resolution in the milliseconds. Although providing a wealth of information about the timing of global brain activity, EEG's ability to localize brain activity to distinct regions is hampered by relatively poor spatial resolution and difficulty in localizing subcortical sources that lie below the surface of the brain. MEG is a related technique that, rather than measuring electrical potentials,

uses an array of sensitive magnetometers to measure the magnetic fields generated by the electrical activity of the brain. One advantage of this is that MEG measurements are not as distorted by the skull and surrounding tissue as those in EEG, thus considerably improving the localization of the source of neural activity.

To examine the precise timing of psychological processes, researchers general employ event-related averaging of different trials of a task to generate a comparatively noise-free waveform representing task-induced brain activity during an experiment. This method, known as event-related potentials (ERPs), has been used to investigate the relative timing of different psychological processes such as face perception (Bentin, Allison, Puce, Perez, & McCarthy, 1996), memory recognition (Curran, Schacter, Johnson, & Spinks, 2001), as well as social categorization and prejudice (Ito, Thompson, & Cacioppo, 2004). With respect to research on self-regulation, various ERP components have been found to be associated with different self-control processes. For instance, there are ERP components that reliably index conflict monitoring (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Nieuwenhuis, Yeung, van den Wildenberg, & Ridderinkhof, 2003), response inhibition (Fallgatter & Strik, 1999), and the emotionally aversive side of self-control conflict and performance errors (Hobson, Saunders, Al-Khindi, & Inzlicht, 2014). ERP has also been used to identify differences between successful and unsuccessful self-regulators. For example, in a study of dieters freely viewing images of tempting food, those who were incentivized to regulate their food choices to lose weight demonstrated ERP evidence of both increased attentional control and reduced value given to unhealthy foods (Harris, Hare, & Rangel, 2013).

Transcranial Magnetic Stimulation

TMS is a noninvasive technique that allows for the creation of temporary “lesions” in relatively circumspect brain regions by disrupting the ongoing electrical activity of a patch of cortex. This is achieved via a powerful magnetic field that, when rapidly switched on and off, induces an electrical current in a small area of the brain directly beneath the magnetic coil. One commonly used technique, known as repetitive TMS, delivers multiple pulses over a short period of time, thereby temporarily disrupting a given area of the brain following the stimulation. One of the advantages of this method over other techniques is its ability to show the causal role that different brain regions play in perceptual, motor, or cognitive processes. For instance, whereas studies using fMRI have shown that a region of the brain known as the intraparietal sulcus is implicated in action observation and planning, TMS was used to demonstrate a direct role for this region in action planning, namely, by

showing that transient disruption of the intraparietal sulcus impairs the ability to form the appropriate hand configurations for grasping objects (Tunik, Frey, & Grafton, 2005).

With respect to research on self-regulation, TMS has been used to demonstrate a causal role for the lateral prefrontal cortex (PFC) in impulsive decision-making (Chambers et al., 2006; Knoch, Pascual-Leone, Meyer, Treyer, & Fehr, 2006) and the preference for immediate rewards over larger delayed ones (Figner et al., 2010). Other studies have shown that deactivation of this region impairs the ability to resist monetary temptations and turn down unfair monetary offers (Baumgartner, Knoch, Hotz, Eisenegger, & Fehr, 2011; Knoch, Schneider, Schunk, Hohmann, & Fehr, 2009).

Magnetic Resonance Imaging of Brain Anatomy

High-resolution magnetic resonance imaging allows for the noninvasive measurement of neuroanatomical structures and connections between structures. Analysis of brain morphometry refers to the measurement of the size, volume, and shape characteristics of different brain structures and tissue types. For example, morphometric methods have been used to study the volume and density of gray matter, where most of the neuronal computations occur, but also of white matter, a tissue type composed primarily of myelinated axons that connect different gray matter areas. Historically the analysis of brain morphometry has been instrumental in much of the successes of MRI in identifying and localizing brain pathologies. Although there are multiple types of analyses that can be carried out on anatomical imaging data, two popular approaches are the morphometric analysis of brain anatomy (including gray matter density, cortical thickness, and volumetric measurements of brain structures) and the analysis of white matter connectivity using diffusion tensor imaging (DTI) (see next section).

With regards to the former, studies have shown that the size and volume of different neural structures are correlated with learning and experience. For instance, musicians have been found to have increased gray matter density in Broca's area (a region important for language) compared to nonmusicians (Sluming et al., 2002), London taxi cab drivers have a larger posterior hippocampus than matched control subjects (Maguire et al., 2000), and experienced meditation practitioners have increased cortical thickness in brain regions involved in attention (Lazar et al., 2005) and lateral prefrontal regions implicated in cognitive control (Kang et al., 2013).

Several studies have examined the relationship between brain morphometry and individual differences in self-regulation abilities. Research on fear extinction, for example, demonstrates that individual differences in the cortical thickness of the ventromedial PFC is positively correlated with the ability to extinguish conditioned fear memories (Milad et al., 2005;

Rauch et al., 2005). Meanwhile, research in other domains has shown that reduced cortical thickness in the lateral PFC is associated with impulsivity (Schilling et al., 2012) and emotional reactivity (Foland-Ross et al., 2010). With respect to what these findings mean for self-regulation more generally, what these studies suggest is that individual differences in self-regulatory success may in part be attributable to differences in the cortical thickness of brain regions important for self-control and executive function.

Diffusion Tensor Imaging

Unlike morphometric methods which can only provide information regarding size and volume of gray and white matter regions, DTI along with methods for determining the direction and integrity of the white matter tracts that connect different brain regions (ie, tractography) allows for inferences regarding the strength and amount of connections linking different brain areas together. Analysis of the white matter connectivity between prefrontal brain regions involved in self-control and striatal regions implicated in reward processing have resulted in novel findings regarding how the connectivity between these systems supports self-regulation-related abilities. For example, individual differences in the ability to forgo immediate rewards for future larger ones (eg, delay discounting) is associated with increased integrity in a fronto-striatal white matter track connecting the striatum to the medial prefrontal (Peper et al., 2013) and lateral prefrontal (van den Bos, Rodriguez, Schweitzer, & McClure, 2014) cortices. Finally, recent work has also demonstrated that the integrity of a white matter pathway between the lateral PFC and a region of the orbitofrontal cortex (OFC) involved in reward processing has been shown to be inversely related to overall body mass index (BMI). What these data suggest is that long-term weight control is associated with individual differences in the strength of the pathway connecting brain areas involved in self-control and those involved in reward processing. One somewhat speculative interpretation of this finding is that the strength of the white matter pathway linking brain regions involved in self-regulation and those related to reward may be just as important as self-regulatory capacity or reward reactivity (Chen, Chavez & Heatherton, unpublished).

Functional Magnetic Resonance Imaging

Although many readers will no doubt be familiar with functional MRI as a means of localizing brain activity associated with stimulus or task conditions, there are many other methods that rely on the same measurement but go beyond basic brain activation studies. For instance, fMRI measurements can be used to make inferences regarding functional connectivity

changes associated with different psychological processes or task parameters. In this type of analysis, it is not the overall magnitude of a brain region that is being measured but rather how the connectivity between a brain region and the rest of the brain changes as a function of different psychological processes. There are also methods for investigating how the brain encodes stimulus properties or task parameters in multivariate patterns of brain activity as well as studies aimed at decoding stimulus properties or psychological processes from fMRI measurements. There is also research that seeks to relate parameters derived from computational models of behavior to levels of brain activity within discrete regions. Finally, there is an entire field devoted to studying the human connectome that relies on resting fluctuation in brain activity to make inferences regarding the network properties of different brain systems (Sporns, 2013). Each of these vastly different approaches relies on the same underlying measure of brain activity, namely, the blood oxygen level–dependent response.

A large proportion of the research on the brain basis of self-regulation is based on brain activation studies carried out with fMRI, and in the following sections, we review this work by looking at brain systems implicated in craving and reward processing, as well as those involved in self-control and response inhibition.

Functional Neuroimaging Studies of Reward

In both animals and humans, a system of brain regions comprising the ventral striatum, OFC, and the ventral tegmental area (VTA) has been associated with reward-related processes (Berridge & Robinson, 2003; Haber & Knutson, 2010; Kringelbach, 2005). For instance, during reward learning in animals, neurons in the VTA show an increased firing rate for unexpected or novel rewards, and after learning to associate these with a cue, VTA neurons shift their response toward the reward-predicting cue (Schultz, Dayan, & Montague, 1997). In humans, functional neuroimaging research has shown that the OFC and ventral striatum show increased brain activity to reward receipt and appear to be sensitive to momentary changes in the subjective value or pleasantness of rewards. For example, when participants consume an appetizing food, their ratings of pleasantness decrease as they approach satiety and this decrease in pleasantness is correlated with decreasing activity in the OFC (Kringelbach, O'Doherty, Rolls, & Andrews, 2003; Small, Zatorre, Dagher, Evans, & Jones-Gotman, 2001).

The OFC and ventral striatum responds not only to reward receipt but also to cues associated with rewards such as money, attractive faces, or food images (Cloutier, Heatherton, Whalen, & Kelley, 2008; Knutson, Taylor, Kaufman, Peterson, & Glover, 2005; van der Laan, de Ridder, Viergever, & Smeets, 2011). For example, the reward system shows heightened activity when listening to preferred passages of music

(Blood & Zatorre, 2001), viewing restaurant menus containing desired food items versus undesired food items (Arana et al., 2003), when smokers view smoking paraphernalia (David et al., 2005) or smoking behavior (Wagner, Dal Cin, Sargent, Kelley, & Heatherton, 2011), and when people view attractive faces from the opposite sex (Aharon et al., 2001; Cloutier et al., 2008; O'Doherty et al., 2003). Learning about cues that can predict reward is vitally important for animals and humans alike, as it helps to guide behavior toward those aspects of the environment that are important for survival (eg, food, water, conspecifics) and motivate behaviors that are evolutionary important (eg, reproduction). As humans are constantly bombarded by cues signaling potential rewards (from television and online advertisements to the sight and smell of high-calorie foods at restaurants and food courts), there has been a long-standing interest in examining the relationship between reactivity to cues and addictive or otherwise unhealthy behaviors (eg, Carter & Tiffany, 1999; Sayette, Martin, Wertz, Shiffman, & Perrott, 2001). For instance, research has demonstrated that reward cues capture people's attention (Castellanos et al., 2009; Lochbuehler, Voogd, Scholte, & Engels, 2011) and can elicit craving and positive hedonic thoughts about the desired items (Hofmann, van Koningsbruggen, Stroebe, Ramanathan, & Aarts, 2010; Sayette & Hufford, 1997).

With respect to neural cue reactivity, there have been a number of studies examining the relationship between brain activity to reward cues and various potential markers of poor self-regulation (eg, addiction, BMI, smoking relapse, weight gain). For example, research has demonstrated a link between individual differences in cue reactivity to food and BMI (Rapuano, Huckins, Sargent, Heatherton, & Kelley, 2015). Other work has attempted to use neural cue-reactivity measures to predict poor self-regulation behavior. For example, Demos, Heatherton, and Kelley (2012) used a food-cue reactivity paradigm to investigate whether individual differences in reward-related brain activity was associated with weight gain during the first year of college (eg, the infamous "freshman 15"). The authors found that food cue-related activity in the ventral striatum prospectively predicted the magnitude of weight gain 6 months later. Moreover, this effect was specific to food images, as the ventral striatal response to other image categories (eg, alcohol, erotic images) was not predictive of the amount of weight gained (Demos et al., 2012).

More recently, Lopez, Hofmann, Wagner, Kelley, and Heatherton (2014) extended this work by combining functional neuroimaging of cue reactivity with an experience sampling paradigm to better understand how cue reactivity is associated with those daily behaviors that contribute to weight gain. In this study, participants first took part in a functional neuroimaging session whereby they viewed images of highly appetizing food items. Subsequent to this, they underwent a period of experience

sampling whereby their daily food desires, amount eaten, and ability to resist acting upon their food desires was measured. The authors found that individual difference in ventral striatal activity to food images predicted both daily food desires and the likelihood of giving in to those desires. Taken together, the results of these studies suggest that individual differences in reward reactivity may be an important source of variance in self-regulatory ability.

Functional Neuroimaging Studies of Self-Regulation

Research on the brain systems involved in the effortful regulation of cravings, emotions, and behavior have largely converged on a system of prefrontal brain regions comprised of regions of the lateral PFC (including the inferior frontal gyrus and ventrolateral PFC) and, particularly in studies of emotion regulation, the ventromedial PFC [for reviews, see (Aron, Robbins, & Poldrack, 2014; Cohen & Lieberman, 2010; Kelley et al., 2015; Ochsner, Silvers, & Buhle, 2012)]. Across multiple tasks and domains, these regions are associated with downregulating reward-related responses to cigarettes (Kober et al., 2010), food (Giuliani, Mann, Tomiyama, & Berkman, 2014; Hare, Camerer, & Rangel, 2009), drugs (Volkow et al., 2010), and monetary rewards (Delgado, Gillis, & Phelps, 2008), and also in downregulating emotional responses to negative emotional stimuli (Johnstone, van Reekum, Urry, Kalin, & Davidson, 2007; Ochsner et al., 2004; Urry et al., 2006). The flip side of these findings is that people suffering from self-regulation impairments will often show enhanced reward or emotion reactivity in conjunction with reduced recruitment of the lateral or ventromedial PFC (eg, Johnstone et al., 2007; New et al., 2007; Silbersweig et al., 2007; Yoo, Gujar, Hu, Jolesz, & Walker, 2007). However, this pattern of findings is not always consistent across the literature, with several studies also showing enhanced lateral or ventromedial PFC activity among those demonstrating self-regulation impairments [see Kelley et al. (2015) for further discussion of the difficulties inherent in attempting to describe self-regulation failure in terms of simple increases or decreases in PFC activity].

More recent work has explored the possibility that individual differences in the recruitment of prefrontal structures involved in self-control may underlie real-world self-regulation impairments. For instance, in a study examining regular smokers attempting to quit smoking, activity in the lateral PFC during a response inhibition task was found to predict reductions in cigarette craving and consumption during a 3-week period (Berkman, Falk, & Lieberman, 2011). In another study, this time in dieters, lateral PFC activity in a similar response inhibition task involving appetitive food images predicted dieters' success at regulating daily food desires over the subsequent week (Lopez et al., 2014). Together with studies demonstrating that inhibiting the electrical activity of the lateral PFC activity

with TMS increases impulsivity during decision-making (reviewed in a previous section), these findings point to the lateral PFC as being vitally important for the regulation of behavior during daily life. Indeed, patients with damage to this area struggle with planning, and are easily distracted by competing cues or task demands (Petrides & Milner, 1982; Shallice & Burgess, 1991).

THE COGNITIVE NEUROSCIENCE OF EGO DEPLETION

Cognitive neuroscience research on ego depletion is still in its relative infancy; however, in the last several years, there have been a number of studies designed to investigate how ego depletion impacts brain system that involves in self-control, affect, and reward. The first of these studies (Inzlicht & Gutsell, 2007) used ERP (for a brief overview of this method, see an earlier section of this chapter) and examined error-related negativity, an index of conflict monitoring thought to originate in the anterior cingulate cortex. In this study, participants performed a standard sequential task paradigm whereby a subset of participants engaged in an effortful emotion regulation task followed by a Stroop task. Relative to a control group, depleted participants showed a decrement in behavioral performance on the Stroop task (ie, an increase in the reaction time difference between incongruent and congruent trials) and a reduced error-related negativity signal. Moreover, the reduction in error-related negativity mediated the relationship between ego depletion and Stroop performance. Based on these findings, the authors suggest that ego depletion is a result of an impaired conflict monitoring process, and thus depleted participants' impaired performance is because they are less able to monitor for commission of an error (Inzlicht & Gutsell, 2007). However, a subsequent study using fMRI instead suggests that depletion appears not so much to reduce conflict monitoring but to disrupt the ability to implement self-control (Hedgcock, Vohs, & Rao, 2012). In this study, half of the participants were assigned to perform an effortful attention control task, whereas the other half performed a similar task that did not require effortful self-control. Following this depletion manipulation, participants engaged in a choice task whereby they were asked to make decisions between various items. Their principal finding was a reduction in right dorsolateral PFC among the depleted group; however, there was no difference in activity between depleted and control participants in the anterior cingulate cortex. The authors interpret this finding as indicating that depletion impairs the ability to implement self-control rather than impairing conflict monitoring (Hedgcock et al., 2012). One possibility for the discrepancy between the prior study and this one is that different self-control tasks tax conflict monitoring and self-control differentially. Whereas performance in the Stroop task used

in the prior study may be predicated on an ability to detect the response conflict between the color of the word and the word itself, the choice task used to assess ego depletion in this study may not be contingent on the ability to successfully monitor for errors but rather is weighted more toward the ability to implement effortful self-control. Indeed, an examination of the behavioral data showed that participants in the depletion condition made faster decisions during the choice task, suggesting that they spent less time deliberating over those decisions (Hedgcock et al., 2012).

Similar findings were observed in another study in which participants engaged in a verb generation task after being assigned to either a depletion condition (consisting of an effortful working memory task) or a control condition. Here, the authors found that activity in the left lateral PFC was reduced in depleted participants compared to the control group, and this reduction in activity was associated with poor performance among the depleted group (Persson, Larsson, & Reuter-Lorenz, 2013). Around the same time, Friese, Binder, Luechinger, Boesiger, and Rasch (2013) published a study demonstrating ego depletion's impact on activity in the lateral PFC by investigating how activity in the same patch of cortex changes during a sequential task paradigm. As in Inzlicht and Gutsell (2007), participants in this study were first tasked with suppressing their emotions, followed by a Stroop task. Whereas ego depletion led to increased reaction times on incongruent trials for the depletion group in the Inzlicht and Gutsell study (2007), here depletion led to higher error rates on incongruent trials but no reaction time differences between depleted and control participants (Friese et al., 2013). With respect to ego depletion's effects on brain activity, the authors found an interaction in the dorsolateral PFC between task and group such that this region showed more activity in the depleted group relative to the control group during the emotion suppression task, but less activity in the depleted group during the Stroop task. Of particular note is that, hitherto, most studies have examined the after-effects of depletion on the brain; however, this study examined the same area of the lateral PFC during both the depletion task and the subsequent task, thereby demonstrating that the same area of lateral PFC is involved in both tasks and is differentially affected by prior effort.

All of the above studies have primarily examined the aftereffects of ego depletion on cognitive tasks (eg, the Stroop or a choice-making task). However, recent experimental work has suggested that ego depletion may have independent effects on self-control and impulse strength, both impairing self-control and intensifying desires and emotions. For instance, prior work by Schmeichel, Harmon-Jones, and Harmon-Jones (2010) showed the ego depletion increases attention to rewards in the absence of any self-control task (Schmeichel et al., 2010). The idea that depletion may independently increase the strength of impulses and rewards is consistent with prior work showing that ego depletion leads people to eat more food (Hofmann, Rauch, & Gawronski, 2007; Vohs & Heatherton, 2000),

drink more alcohol (Muraven, Collins, & Nienhaus, 2002), and show difficulty regulating their emotions (Schmeichel, 2007). Although the findings in each of these studies were initially interpreted as being the result of impaired self-regulation capacity, it is also possible to view these findings as examples of increased impulse strength.

Two neuroimaging studies of ego depletion have sought to address the possibility that depletion affects not only the self-control side of the equation but also the impulse side. In the first of these, participants completed a simple emotional scene categorization task, followed by either an effortful attention control task or noneffortful version of the same task. Subsequent to this, they completed another set of emotion scene categorizations (Wagner & Heatherton, 2013). Of interest here is whether depletion resulted in an exaggerated response in regions of the brain that are sensitive to emotional valence and intensity (ie, the amygdala). Compared to their pre-depletion baseline, depleted participants demonstrated an increased amygdala response to negative emotional scenes but not to neutral or positive scenes. Moreover, the difference between depleted and control participants was significant for negative emotional scenes, but not for neutral or positive scenes. Importantly, by assessing amygdala reactivity to emotional scenes prior to depletion, the authors were able to demonstrate that there was no pre-existing difference between the groups. In addition to these findings, this study also examined the functional connectivity between the amygdala and a region of the ventral medial PFC that has been implicated in emotion regulation (Johnstone et al., 2007; Somerville et al., 2013). The results showed that, relative to controls, depleted participants exhibited a reduced coupling between the amygdala and VMPFC (Wagner & Heatherton, 2013) suggesting the possibility that, unlike controls, depleted participants fail to spontaneously recruit the VMPFC to downregulate reactivity to negative and aversive emotional scenes.

A second functional neuroimaging (ie, Wagner, Altman, Boswell, Kelley, & Heatherton, 2013) showed a conceptually similar finding, this time in the domain of dieting and food cue reactivity. Here, chronic dieters were exposed to appetizing food images following the same ego depletion manipulation as in the above study. Compared to nondepleted dieters, those that underwent ego depletion demonstrated a heightened reward-related response to food images in the OFC. Moreover, analysis of the functional connectivity between this region and the lateral PFC found evidence of reduced connectivity between these areas relative to a control group (Wagner et al., 2013). These two studies suggest that, even in the absence of explicit self-control tasks, ego depletion may serve to heighten impulses and emotions (see also Chapter 6 for an extended discussion of this possibility). Moreover, it appears that the mechanism for this increased reactivity is due to a decoupling between regulatory regions in the PFC and the cortical and subcortical regions involved in emotion and reward.

Taken together, all the ego-depletion studies reviewed earlier are generally consistent with a balance model of self-regulation failure (eg, [Heatherton & Wagner, 2011](#)). In this framework, prefrontal regions involved in self-regulation are common across many form of self-regulation, however, the target of prefrontal control differ according to the individual's regulatory context. For instance, if an individual is regulating fear or anger, then a prefrontal–amygdala pathway may be involved, whereas if an individual is regulating food cravings, this may instead involve a prefrontal and ventral striatal/orbitofrontal circuit. In this model, self-regulation failure occurs whenever the strength of an impulse (represented in the reward or emotional systems) outmatches current self-regulatory capacity, or whenever self-regulatory capacity is itself diminished, be it due to depletion, prefrontal brain damage, distraction, or alcohol. The studies reviewed here are consistent both with the notion that ego depletion somehow disrupts the ability to recruit prefrontal mechanisms for self-control, but also that depletion may decouple this system from those involved in representing reward value or emotional salience. Once uncoupled, these regions become sensitized to the rewarding properties of stimuli, which in turn can lead to further difficulties engaging in self-regulation.

Finally, it is worth noting that although the results across these few ego-depletion studies are generally consistent with each other, there are still some issues remaining to be resolved. For example, the first set of studies used primarily cognitive tasks (eg, the Stroop task) to assess the aftereffect of depletion. These studies have generally shown that ego depletion leads to reduced recruitment of the anterior cingulate cortex ([Inzlicht & Gutsell, 2007](#)) or the lateral PFC, although there remains some ambiguity as to the laterality of these effects, with some studies demonstrating reductions in left lateral PFC ([Persson et al., 2013](#)) and others in right lateral PFC ([Friese et al., 2013](#); [Hedgcock et al., 2012](#)). Moreover, in other studies ([Wagner et al., 2013](#); [Wagner & Heatherton, 2013](#)), depletion does not act directly on the overall amount of activity in a region, but rather appears to reduce the connectivity between regulatory regions in the PFC and their targets in the reward or emotion brain systems. Whether these differences represent separate phenomena or are instead due to differences in tasks or analysis methodology remains an ongoing question.

ALTERNATIVE THEORIES OF EGO DEPLETION

Recently, a number of alternative explanations for the ego-depletion effect have been proposed ([Beedie & Lane, 2012](#); [Inzlicht & Schmeichel, 2012](#); [Job et al., 2010](#); [Kurzban, Duckworth, Kable, & Myers, 2013](#)). Common among them is the notion that self-regulation failure following depletion may reflect not so much a lack of self-control capacity, but rather a decision to avoid engaging in further effortful task performance in favor of expending

less effort. Underlying this theory is the notion that expending effort is itself aversive and to be avoided, unless the rewards are sufficient. For instance, research has shown that, all things being equal, people will invariably prefer tasks that they perceive as requiring less effort (Kool, McGuire, Rosen, & Botvinick, 2010). These new ways of thinking about depletion recast the classic tug-of-war between impulses and self-control capacity as a labor dispute whereby effortful cognitive work will be performed by the individual only as long as the payment is sufficient. In this framework, the after-effects of depletion are due to insufficient reward for cognitive services rendered. Functional neuroimaging work has provided evidence that the lateral PFC may be involved in registering the cost of engaging in effortful tasks. For instance, when participants were given a choice to choose between tasks that differed in the overall effort required to complete them, participants came to prefer the low-effort task, and activity in the LPFC during the task block was associated with subsequent ratings of how much they wanted to avoid the effortful task (McGuire & Botvinick, 2010).

That is not to say these accounts are not without some issues of their own when it comes to attempts to utilize them to explain the constellation of previously reported depletion effects. For instance, given a fixed reward for participants, it would be sensible for them to avoid additional effort on self-control tasks after depletion (assuming minimally motivated experimental participants). However, it is difficult to reconcile this view with findings showing that depletion precipitates self-regulation failure in circumstances for which individuals are highly motivated to continue exerting effort irrespective of the task rewards. For example, restrained eaters are highly motivated to avoid the overconsumption of unhealthy food, and yet self-regulatory depletion can lead to disinhibited eating (Vohs & Heatherton, 2000) and increased reward cue reactivity (Wagner et al., 2013). Similarly, people are typically motivated to give a good impression; however, research has shown that, following an effortful self-control task, they become less thoughtful during social interactions, thereby appearing arrogant or socially awkward (Vohs, Baumeister, & Ciarocco, 2005). It is, on the surface, difficult to reconcile these findings with the notion that these participants are, following depletion, choosing to avoid the effortful task of maintaining their diet or not appearing like a schmuck in a social interaction simply because they have been insufficiently rewarded. It instead appears less a case of *will not* and more a case of *cannot*.

CONCLUSION

The last several years have seen a surge of research on brain basis of self-regulatory failure; by and large, this work is consistent with the view that self-regulation may result from a strong impulse or insufficient

self-control capacity. Recent theorizing has suggested that many examples of self-regulation failure may instead be conceived of not as a lack of self-control capacity, but rather as a shift in motivation, as individuals opt to focus on rewards and leisure (Inzlicht & Schmeichel, 2012; Inzlicht, Schmeichel, et al., 2014) or determine that the cost of self-control is too great and therefore decide to avoid expending any more effort (Kool & Botvinick, 2014). Current findings from functional neuroimaging studies are not yet in a position to arbitrate between these different accounts of self-regulation failure, as findings of reduced prefrontal activity (Friese et al., 2013; Hedgcock et al., 2012; Persson et al., 2013) or of alternations in functional connectivity between the PFC and the reward system (eg, Wagner et al., 2013; Wagner & Heatherton, 2013) following depletion are consistent both with the strength model of self-control but also with the various alternative accounts (Inzlicht, Schmeichel, et al., 2014; Kurzban et al., 2013). As the many chapters in this book will attest, there is much more work to be done to elucidate the mechanisms of ego depletion. Given the increasing importance of social and cognitive neuroscience findings in contemporary theories of self-regulation failure and ego depletion, we have no doubt that a neuroscience approach will continue to play an important if not decisive role in our understanding of the phenomena of ego depletion.

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