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The nature of self-regulatory fatigue and “ego depletion”: Lessons from physical fatigue

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Abstract

Self-regulation requires overriding a dominant response, and leads to temporary self-regulatory fatigue. Existing theories of the nature and causes of self-regulatory fatigue highlight physiological substrates such as glucose or psychological processes such as motivation, but these explanations are incomplete on their own. Historically, theories of physical fatigue demonstrate a similar pattern of useful but incomplete explanations, as recent views of physical fatigue emphasize the roles of both physiological *and* psychological factors. In addition to accounting for multiple inputs, these newer views also explain how fatigue can occur even in the presence of sufficient resources. Examining these newer theories of physical fatigue can serve as a foundation on which to build a more comprehensive understanding of self-regulatory fatigue that integrates possible neurobiological underpinnings of physical and self-regulatory fatigue, and suggests the possible function of self-regulatory fatigue.

Keywords

self-regulation; ego depletion; fatigue; central governor; physical fatigue

The ability to self-regulate—control one's thoughts, emotions, or behaviors by overriding a dominant response—is crucial for a wide variety of behaviors that have socially important outcomes, including mental health, physical health, academic success, and relationship quality (Baumeister, Heatherton, & Tice, 1994; Tangney, Baumeister, & Boone, 2004). Without the capacity to override one's impulses, most goal-directed behavior would be impossible. One particularly influential theory of self-regulation is the strength model (SM), which is based on the principle that all acts of self-regulation rely on a common and limited energy source (Baumeister, Vohs, & Tice, 2007). According to this view, self-regulatory effort drains strength and leads to temporary self-regulatory fatigue or “ego depletion”

(Baumeister, Bratslavsky, Muraven, & Tice, 1998, p. 1252), which in turn causes regulatory failure.

There are several compelling aspects of the SM account of self-regulation. First, there is a large body of empirical support for the predictions of the SM, including a meta-analysis of 83 studies that employed the sequential-task paradigm, an experimental procedure in which an initial self-regulatory task purportedly depletes self-regulatory energy and leads to impaired performance on a subsequent self-regulatory task (Hagger, Wood, Stiff, & Chatzisarantis, 2010; cf., Carter & McCullough, 2013). Second, as a metaphor for both trait and state self-regulatory strength and fatigue, the SM parsimoniously accounts for why some people tend to regulate better than others (i.e., stronger people), as well as the circumstances under which one is likely to falter at self-regulation (i.e., after exertion). Third, the SM integrates mental and physical regulation by identifying a limited physiological substrate necessary for both, an idea that is elegant and intuitively appealing. People sense that self-regulation requires work or effort, and that mental fatigue follows periods of mental work just as physical fatigue follows bouts of physical work.

Despite its intuitive appeal and the considerable body of empirical support for its predictions, the SM has some weaknesses. It cannot explain recent findings that people are able to effectively self-regulate after being “depleted”, nor does it adequately account for the role of motivation in self-regulatory performance. The SM also remains unclear regarding the inputs, outputs, and mediating mechanisms of self-regulatory fatigue. As an alternative that builds on the SM, current knowledge about the causes and moderators of physical fatigue (e.g., Central Governor Theory; Noakes, 1997) provides an instructive parallel for understanding the nature and causes of self-regulatory fatigue. In both physical fatigue and self-regulatory fatigue, humans behave *as if* resources were limited, despite the fact that they may not be. Physical fatigue and subsequent cessation of muscular contractions may occur in the absence of any depletion of physiological substrates (Noakes, 1997; Noakes, Gibson, & Lambert, 2005). In addition, there are multiple inputs that determine the experience of physical fatigue, including both motivational states and physiological resources. Increased consideration of these two qualities of physical fatigue—multiple determination and dissociation between fatigue and resources—informs an understanding of self-regulatory fatigue that is consistent with empirical findings and generates new directions for research in self-regulatory fatigue.

First, a brief history of the SM is presented that describes its evolution through several different iterations or versions. Next, the proposed physiological and psychological mechanisms in the SM, along with strengths and weaknesses of each are discussed. A similar history of explanations for physical fatigue is described, followed by evidence for similarity to self-regulatory fatigue. Finally, we discuss possible neurophysiological underpinnings of physical fatigue and self-regulatory fatigue, speculate on why fatigue might occur in the presence of sufficient resources, and expand future directions for testing a model of self-regulatory fatigue based on what is known about physical fatigue.

A Brief History of the Strength Model: Motivation, Muscle, and Glucose

One question that has vexed self-regulation research is why people sometimes resist temptations successfully but at other times fail. A particularly influential explanation for this phenomenon is that there must be depletion of some energy source required for overriding dominant responses or impulses (Baumeister et al., 1994). Based in part on observations that participants performed more poorly on a self-regulatory task (e.g., emotional suppression) when it was preceded by another self-regulatory task (e.g., controlling attention) than when it was preceded by a non-self-regulatory task (i.e., one that is automatic or overlearned such as mental arithmetic), self-regulatory fatigue began to be described as a process of energy depletion analogous to muscle failure (Baumeister et al., 1994; Muraven, Baumeister, & Tice, 1999). Specifically, what came to be known as the “strength model” (SM) proposed that the act of regulating one's cognitions, behaviors, or emotions relies on a common and limited energy source that is temporarily used up as a result of engaging in prior acts of self-regulation, in the same way that skeletal muscles become fatigued and unable to sustain work as a result of prior exertion.

Earlier accounts emphasized the role of acquiescence or an active decision to stop regulating as responsible for self-regulatory failures, rejecting any role for energetic substrates, either metaphorical or literal (Baumeister & Heatherton, 1996; Heatherton & Baumeister, 1996). At that time, the model operated under the assumption that there were no irresistible impulses outside of basic biological needs such as breathing, urinating, and sleeping (Baumeister & Heatherton, 1996). In other words, quitting a challenging task did not occur due to exhaustion or depletion, but was due rather to the competing motivation to reduce discomfort or frustration.

Later accounts explained self-regulatory failure not as a form of active acquiescence but rather as a problem of resource insufficiency (Baumeister et al., 1998). The metaphor of muscle fatigue and failure began to appear shortly thereafter (Muraven et al., 1999; Muraven & Baumeister, 2000). The muscle metaphor gained support when it was demonstrated that in addition to the temporary fatiguing effect following a self-regulatory activity, repeated bouts of self-regulatory activities over days or weeks appeared to improve one's baseline level of self-regulatory strength, much in the same way that exercising a muscle increases strength (Muraven et al., 1999).

A series of studies returned the emphasis to motivational factors, demonstrating that increasing intrinsic motivation to perform a task, as well as providing monetary or altruistic incentives, improved self-regulatory performance (Moller, Deci, & Ryan, 2006; Muraven, Gagne, & Rosman, 2008; Muraven & Slassareva, 2003; Vohs, Baumeister, & Schmeichel, 2012). Extending the focus on motivational factors, the next wave of studies found that people could be motivated to conserve their regulatory resources if they expected future regulatory demands (Muraven, Shmueli, & Burkley, 2006; Tyler & Burns, 2008). However, perhaps due in part to the popularity and intuitive appeal of the muscle metaphor, the SM began to swing back toward the resource depletion approach and search for the physiological substrates—or rather, lack thereof—responsible for self-regulatory failure, settling on glucose (Gailliot et al., 2007; Gailliot, Peruche, Plant, & Baumeister, 2009; Masicampo &

Baumeister, 2008). This latest version of the SM is hereafter referred to as “the glucose depletion hypothesis,” though all modern variations of the SM are resource depletion models in that they identify substrate insufficiency as the ultimate cause of self-regulatory failure. Based on the assumption that skeletal muscles become fatigued during physical exercise because they have used up available glucose, the claim of the glucose depletion hypothesis was that insufficient glucose was responsible for both muscle fatigue and self-regulatory fatigue (Baumeister et al., 2007; Gailliot et al., 2007). The brain requires glucose to perform cognitive functions (Sieber & Traystman, 1992), and preliminary evidence found increases in glucose oxidation after complex tasks requiring mental effort (Fairclough & Houston, 2004). Furthermore, a series of nine studies suggested that self-regulatory tasks decreased blood glucose relative to non-self-regulatory tasks, and that replenishing glucose via a sugar (vs. placebo) drink resulted in improved performance on a subsequent self-regulatory task (Gailliot et al., 2007). Several other studies found similar effects for the ability of oral glucose administration to prevent self-regulatory fatigue (Dewall, Baumeister, Gailliot, & Maner, 2008; Gailliot et al., 2009; Masicampo & Baumeister, 2008), including one study examining self-regulation in the form of persistence among dogs (Miller, Pattison, DeWall, Rayburn-Reeves, & Zentall, 2010). However, there was recognition that the glucose depletion hypothesis could not account for a host of findings, such as those showing post-sleep improvements in self-regulatory performance without a concomitant increase in blood glucose levels (Baumeister et al., 1994; Mednick et al., 2002; Takahashi & Arito, 2000). In response, a slight variation of the glucose depletion hypothesis was proposed that focused on brain glycogen—the stored form of glucose that can be converted to glucose when needed—as the depletable substrate required for self-regulation (Gailliot, 2008).

Most recently, the shift in explaining self-regulatory fatigue has again leaned toward motivation and resource *allocation* rather than resource *availability*. A series of papers provided compelling evidence that self-regulatory ability may not actually be limited, arguing that engaging in self-regulation triggers a shift in motivation and attention that make self-regulatory failure more likely in a subsequent task (Inzlicht & Schmeichel, 2012; Inzlicht & Schmeichel, 2013; Inzlicht, Schmeichel, & Macrae, 2014). Specifically, engaging in self-regulation on Task 1 reduces motivation to exert self-regulation on Task 2 and increases motivations to act on impulse; likewise, there is reduced attention to cues signaling control and increased attention to reward following self-regulatory exertion. This model suggests that, first, participants who exert more self-regulatory effort feel more justified to “slack off” during subsequent tasks (Kivetz & Simonson, 2002) and, second, that most laboratory self-regulation tasks do not provide rewards for good performance; those that do, find reduced self-regulatory fatigue (Moller et al., 2006; Muraven et al., 2008; Muraven & Slassareva, 2003).

With a similar emphasis on resource allocation, other recent models posit that the sensation of self-regulatory fatigue results from complex mental calculations regarding opportunity costs, which are the lost benefits associated with bypassing a different activity. Such benefits are diverse and might include skill acquisition, social connection, or merely entertainment. In this view, when opportunity costs for other activities are high, meaning the next best option is close in value to the chosen activity, self-regulatory fatigue will motivate switching from the current activity to the next best alternative (Kurzban, Duckworth, Kable, & Myers,

2013). An opportunity-cost model would predict “that doing math problems in the presence of the smartphone will be perceived as more effortful than when the smartphone is absent because opportunity costs are higher” (Kurzban et al., 2013, p. 666). This seems to be a variation of the argument that mental fatigue is a form of goal conflict (Hockey, 2011), and is consistent with the view that mental resources are limited due to allocation rather than depletion (e.g., Kahneman, 1975).

The recent shift back toward motivation is encouraging insofar as self-regulation is a complex activity and is likely influenced by motivational components. However, a review of the history of self-regulation reveals that models have largely been entirely motivationally based or physiologically based, without an integrated model of self-regulation that takes both physiological and motivational factors into account. In the next section, the physiological and psychological mechanisms that have been proposed to constitute self-regulatory fatigue are reviewed, along with strengths and weaknesses of those explanations. This is followed by a review of how the tension between physiological and psychological explanations has been explored in the physical fatigue literature. Finally, an argument is made for using what is known about physical fatigue to advance our understanding of self-regulatory fatigue.

Strengths and Weaknesses of the Physiological Mechanisms in the Strength Model

The glucose depletion hypothesis, which proposes that a lack of glucose is the reason for self-regulatory failure, is an idea that has several strengths. For one, it is intuitively appealing, because the phenomenology of self-regulatory fatigue is such that one feels as if something were running out. Furthermore, self-regulation is associated with physiological changes in parasympathetic nervous system activity normally associated with resource conservation. Self-regulatory tasks also correlate with energetically conservative changes in the heart, liver, and immune system (e.g., Eisenlohr-Moul, Fillmore, & Segerstrom, 2012; Kennedy & Scholey, 2000; Scholey, Harper, & Kennedy, 2001; Segerstrom & Miller, 2004; Segerstrom, Smith, & Eisenlohr-Moul, 2011). Thus, physiologically speaking, the body behaves as if biological resources were limited and resource conservation was important for self-regulation.

Despite these strengths, the glucose depletion hypothesis has significant weaknesses and has recently fallen out of favor for several important reasons (e.g., Beedie & Lane, 2011; Kurzban, 2010). Testing the validity of the glucose depletion hypothesis requires demonstrating that self-regulatory tasks decrease glucose relative to baseline (rather than relative to a non-self-regulatory task), but this contrast was not tested in the studies that supported this hypothesis, and more recent research has shown that normative fluctuations in blood glucose make this necessary proposition unlikely (Molden et al., 2012). The amount of total brain energy expended on any one cognitive task is negligible, and unlikely to result in noticeable (or measureable) decreases in peripheral blood glucose (Beedie & Lane, 2011; Clarke & Sokoloff, 1998; Kurzban, 2010). These findings also cast doubt on the glycogen version of the glucose depletion hypothesis because there would be little need for the brain

to convert glycogen to glucose to perform mental tasks, particularly as brief (~5 minutes) as those used in the relevant studies. Even during high intensity physical exercise, brain glycogen levels are reduced but likely not responsible for exercise termination (Secher, Seifert, & Van Lieshout, 2008).

The rate of absorption of glucose is also inconsistent with the empirical findings. Simply rinsing one's mouth with a glucose solution and then spitting it out before ingestion results in improved self-regulation on a task administered immediately afterward (Molden et al., 2012; Sanders, Shirk, Burgin, & Martin 2012). Glucose is absorbed almost entirely in the gut, so it would be impossible for glucose briefly swished in the mouth to cause an increase in available blood glucose (Gunning & Garber, 1978). These findings rebuff the claim that glucose or glycogen depletion causes self-regulatory fatigue, suggesting instead that glucose may provide a signal value regarding the expected availability of energy. Supporting this possibility, it has been found that oral administration of glucose but not artificial sweeteners activates reward centers in the brain (e.g., anterior cingulate, striatum), probably via a class of carbohydrate-specific receptors in the oral cavity (Chambers et al., 2009). The glucose depletion hypothesis fails to account for the findings that performance on some complex mental tasks, such as those involving response time, *improves* after vigorous physical exercise, which is associated with decreases in levels of blood glucose (Hillman, Erickson, & Kramer, 2008; Hillman et al., 2009; Kurzban, 2010; Tomporowski, 2003).

Finally, although some animal model studies suggest that reductions in brain glucose can occur due to complex cognitive tasks, there are several reasons why these findings may not apply to self-regulatory fatigue in humans. One study found that extracellular glucose levels in the hippocampus of rats declined by 31% during a cognitively demanding maze task versus an 11% decline during a less demanding maze task, and that glucose administration prior to the maze task improved performance only on the complex maze (McNay, Fries, & Gold, 2000). Although the authors argue that the complex maze task is a “working memory task” for rats, it is not analogous to a self-regulatory task in humans, in which a dominant response is overridden. Second, the glucose decline was found only in the hippocampus, an area of the brain typically associated with memory consolidation rather than self-regulatory functions, which are more often associated with the frontal cortex in humans (Cohen & Lieberman, 2010; see *Potential Physiological Mechanisms of Fatigue*, below). Finally, there was an 11% decline in glucose among the rats presented with the less challenging maze. If glucose depletion caused performance decrements, it seems reasonable to assume that glucose administration would have improved performance in those rats with the 11% decline as well, but there was no improvement in performance among this group. These results suggest that glucose levels in certain parts of the brain may affect performance of some complex cognitive tasks, but they do not support the claim that glucose insufficiency *causes* self-regulatory fatigue.

Beyond the glucose depletion hypothesis, another limited resource version of the SM could still be tenable if it could be shown that depletion of some other physiological substrate is responsible for self-regulatory fatigue. In the more general field of mental fatigue, which examines fatigue due to any mental work rather than focusing exclusively on self-regulation, it has been speculated that fluctuations in levels or concentrations of neurotransmitters such

as dopamine, norepinephrine, serotonin, or some combination of these are responsible for fatigue (Malecek & Poldrack, 2013; for a review, see Meeusen, Watson, Hasegawa, Roelands & Piacentini, 2006). However, there is no evidence that mental fatigue is caused by depletion of any neurophysiological substrates, or that such substrates are even capable of being depleted except in cases of disease or death (Hockey, 2011). For example, some studies employing acute tryptophan depletion (ATD), a pharmacological intervention to temporarily reduce central nervous system serotonin by 80-90%, have demonstrated reduction in performance on some self-regulatory tasks such as dichotic listening tasks and attention regulation (Schmitt et al., 2000). However, the evidence for this effect is mixed, with some studies showing no change or even improvements in performance on self-regulatory tasks following ATD (e.g., Hughes et al., 2003; Mendelsohn, Riedel, & Sambeth, 2009). Furthermore, ATD is a pharmacological procedure that reduces serotonin to extremely low levels that would not normally occur and would therefore have limited applicability to understanding how modestly lowered levels of serotonin or any other neurotransmitter are related to self-regulatory fatigue.

In summary, the intuitively appealing metaphor of the human mind as a battery that can be depleted and recharged has been explored scientifically for over a century (e.g., Thorndike, 1900), yet there is still no convincing evidence for this view. Since that time, some researchers of mental fatigue concluded that the pursuit of the energy depletion model of fatigue was a distraction, choosing instead to focus on motivation and energy allocation (e.g., Bartley & Chute, 1947; Hockey, 2011; Kanfer & Ackerman, 1989). Several facts are not consistent with or accommodated by the SM or the glucose depletion hypothesis: How possible substrates actually act in the body; physiological changes in the entire organism, not just the bloodstream or the brain; and the unusual finding of the effects of swishing glucose (Chambers et al., 2009; Molden et al., 2012; Sanders et al., 2012). However, the strengths of a physiological substrate depletion explanation are that we feel as if something were running out, and that the body behaves as if biological resources were limited. Despite the lack of evidence that substrate depletion *causes* self-regulatory fatigue, availability of physiological substrates might serve among several inputs to a system that governs the experience of both physical fatigue and self-regulatory fatigue.

Strengths and Weaknesses of the Psychological Mechanisms in the Strength Model

A number of studies highlight the importance of motivation and perception for self-regulatory performance phenomena not easily explained by a limited resource model (for a review, see Inzlicht & Schmeichel, 2012). Consistent with the motivational and attentional shift framework reviewed above (Inzlicht & Schmeichel, 2012), when participants are motivated to perform better because they believe their performance will help others or themselves (as when they are given monetary rewards for better performance), they indeed perform better than their less motivated counterparts (Boucher & Kofos, 2012; Muraven & Slassareva, 2003). Similar motivational effects have been found even when the motivation primes are subconscious (Capa, Bouquet, Dreher, & Dufour, 2012). Finally, when participants were made to believe that they would be engaging in a demanding task in the

future, they demonstrated worse persistence on an initial task, an effect attributed to motivation to conserve energy for the future task (Muraven et al., 2006; Tyler & Burns, 2008). It should be noted that some recent studies supporting the SM acknowledge the role that motivational factors can play while still asserting that some form of substrate depletion is ultimately responsible for self-regulatory fatigue (e.g., Vohs et al., 2012). For example, it was shown that increasing motivation from baseline on a self-regulatory task can prevent fatigue at moderate but not high levels (Vohs et al., 2012).

Also difficult to reconcile with the SM or the glucose depletion hypothesis are findings suggesting that simply manipulating participants' perceptions of how fatiguing the tasks are can alter levels of self-regulatory fatigue. For example, participants who erroneously believed they were more fatigued exhibited reduced persistence on a subsequent self-regulatory task compared with those who were made to believe they were less fatigued (Clarkson, Hirt, Jia, & Alexander, 2010). When participants' implicit theories of self-regulation were manipulated, either by having them believe self-regulation was a limited resource or a non-limited resource, those who were made to believe it was limited showed impaired performance on a subsequent task (Job, Dweck, & Walton, 2010). If participants naturally expected self-regulation to rely on a limited resource, challenging those expectancies improved performance (Martijn, Tenbult, Merckelbach, Dreezens, & de Vries, 2002). Participants who naturally hold a non-limited theory of willpower (vs. those who believe it is limited) show better self-regulation outside of the lab (e.g., less unhealthy eating and procrastination) when self-regulatory demands are higher (Job, Walton, Bernecker, & Dweck, 2015).

Perceptions of the qualities of a task can also influence self-regulatory outcomes. Although making choices has been shown to be fatiguing, the effects are canceled out when participants perceive those choices to be autonomous or self-directed (Moller et al., 2006; Vohs et al., 2008). Merely thinking about someone else self-regulating impairs performance more than thinking about someone who is not self-regulating, a phenomenon known as vicarious depletion (Ackerman, Goldstein, Shapiro, & Bargh, 2009). Similar effects are found for vicarious restoration: Thinking about someone engaging in restorative activities leads to subsequent improvements in one's own self-regulatory performance (Egan, Hirt, & Karpen, 2012). If self-regulatory fatigue were due strictly to the depletion of glucose (or any physiological substrate), participants' perceptions of the tasks would have no influence on their objective performance.

A major limitation to the current understanding of psychological and motivational explanations of self-regulatory fatigue is that they lack an ultimate explanation of why motivational shifts occur to begin with. Considering how integral self-regulation is to many aspects of life, existing theories fail to provide an adequate explanation for why it would ever be adaptive to experience self-regulatory fatigue. Although recent motivation theories provide compelling evidence that motivational and attentional shifts happen after Task 1 that make self-regulatory failure more likely on Task 2 (Inzlicht & Schmeichel, 2012), they fail to explain the ultimate function that fatigue serves.

Opportunity cost models attempt to answer this question by suggesting that fatigue serves the function of motivating the organism to switch to the next best available alternative in the environment (Kurzban et al., 2013). Yet, opportunity-cost-only models have significant problems of their own. For one, they fail to account for why rest would ever be chosen over another activity. If self-regulatory fatigue is due simply to the sense that other activities might make better use of one's self-regulatory efforts, people would simply switch from one self-regulatory task to another self-regulatory task with the next best opportunity cost/benefit ratio, rather than disengaging from self-regulatory tasks altogether. As much of the SM literature suggests, switching from one self-regulatory activity to another *does* result in performance declines on the second task (Hagger et al., 2010). Additionally, when participants are given 10 minutes of rest between tasks as opposed to no rest or 3 minutes of rest, self-regulatory performance improves (Tyler & Burns, 2008). According to the opportunity cost model, as total time spent engaged in an experiment increases—whether at rest or engaged in a task—participants would incur higher opportunity cost and therefore demonstrate higher fatigue.

Another problem with opportunity cost models is that they have difficulty explaining why people would ever become fatigued if they were engaging in a high value and high expectancy activity that requires self-regulation. For instance, someone driving a long distance to an important activity should not become fatigued (Hoffmann & Kotabe, 2013). If fatigue indicates a worsening cost/benefit ratio, people should always disengage from that activity, yet people sometimes persist on tasks despite feeling fatigued. Finally, if the fatigue state has the metacognitive function of interrupting the currently active goal to allow others into contention, this fatigue should not persist into the next task as is typically shown in a sequential-task paradigm (Hagger et al., 2010). The fatigue state should disappear immediately after switching tasks if opportunity-cost-only models were correct. For a comprehensive list of arguments against the strict opportunity cost perspective, see commentaries to Kurzban and colleagues (2013).

Taken together, motivation and opportunity cost theories go a long way toward explaining the role of psychological factors in self-regulatory fatigue, and account for a multitude of findings that cannot be explained from a limited physiological resource depletion perspective. Their shortcoming is that they disregard potential inputs from physiological substrates and ultimately fail to explain the function of fatigue. On the other hand, the SM and its glucose depletion hypothesis (or any explanation relying on insufficiency of a physiological substrate) cannot account for the ability of psychological factors such as beliefs and motivation to over-ride self-regulatory fatigue, even when that fatigue is substantial. Several authors have recently expressed a need for “A parsimonious theory [that] would posit a unitary mechanism for maintaining control over the task at hand, whether this entails overcoming neural fatigue in a chess marathon or muscle fatigue in a long distance marathon” (Holroyd, 2013, pg. 694; for similar arguments for a unified system of mental and physical fatigue, see Boksem & Tops, 2008; Iran-Nejada & Zengaro, 2013). Findings in the domain of physical fatigue suggest that self-regulatory fatigue can be understood only by considering both physiological and psychological factors, not just one or the other.

Physical Fatigue: Lessons for Self-regulatory Fatigue

The tension between physiological substrate depletion and psychological explanations of fatigue are not unique to the field of self-regulation. Since myography techniques first allowed measurement of muscle activity in the late 1800s, researchers have emphasized the depletion of local resources—in early studies, oxygen—as responsible for physical fatigue as well (Hill, Long, & Lupton, 1924). Similar theories attributing physical fatigue to a “catastrophic” failure of homeostasis due to a depletion of biological substrates, a buildup of toxins, or both have persisted throughout time, just as they have in the self-regulatory fatigue literature (Hermansen & Osnes, 1972; Hill et al., 1924; Noakes, 1997; Sahlin, Harris, Nylin, & Hultman, 1976). Also as in the self-regulatory fatigue literature, these theories have been challenged by the role of psychological factors. Muscle fatigue has traditionally been defined as the inability to maintain a given level of muscle force output and typically considered to reflect a “catastrophic failure” of homeostasis due to a depletion of substrates, a buildup of toxins, or both (Hermansen & Osnes, 1972; Hill et al., 1924; Noakes, 1997; Sahlin et al., 1976). However, a variety of evidence suggests that these proposed mechanisms could not be directly responsible for muscle fatigue.

Depletion of energetic substrates such as glycogen, glucose, or adenosine triphosphate (ATP, the source of muscle mechanical energy) does not appear to be responsible for exhaustion-induced termination of exercise. Muscle biopsies from cyclists who had exercised at submaximal workload revealed that intramuscular levels of ATP were no different at exhaustion compared to rest and that these levels never dropped below 50% of resting concentrations at any time during the exercise bout, suggesting that fatigue causes people to terminate exercise well before muscle energy reserves are spent (Noakes & Gibson, 2004; Parkin, Carey, Zhao, & Febbraio, 1999). Muscle glycogen stores are also far from being completely used up at exercise-induced exhaustion (Bergström, Hermansen, Hultman, & Saltin, 1967; Coyle, Coggan, Hemmert, & Ivy, 1986; Hermansen, Hultman, & Saltin, 1967). There is no reduction in force output from electrically stimulated samples of *in vitro* skeletal muscle supplied with blood flow, even when muscle acid levels increase to those consistent with exhaustion-induced exercise termination (Westerblad, Bruton, & Lannergren, 1997; Wiseman, Beck, & Chase, 1996). Similarly, transcranial stimulation of the human motor cortex produces muscle contractions that generate more force than that achieved during maximal voluntary contractions (Gandevia, 2001). Cessation of exercise due to exhaustion even in extreme situations such as high altitude or severe heat occurs before any homeostatic dysfunction in metabolic or thermoregulatory systems (Gonzalez-Alonso et al., 1999; Green, Sutton, Cymerman, Young, & Houston, 1989; Nybo & Nielsen, 2001; Parkin et al., 1999). Mental exertion does not alter neuromuscular functioning of the knee extensors, despite the fact that mentally fatigued subjects perceived greater exertion (Pageaux, Marcora, & Lepers, 2013). Furthermore, muscle fatigue begins almost immediately after the onset of exercise; it is highly unlikely that any substrate could be depleted so quickly (Gandevia, 2001). Taken together, these studies suggest that although it is important to consider local factors, fatigue and performance limits are mediated by the central nervous system.

Psychological influences on effort and fatigue indicate that physiological substrates are not the only determinants. Muscle fatigue due to brief anaerobic exertion such as sprints, as well

as endurance endeavors such as marathons, can be moderated by a host of psychological factors, including hypnosis, sudden noises, music, and deception regarding workload, suggesting control by central mechanisms instead of, or in addition to, peripheral energy stores (Hampson et al., 2004; Ikai & Steinhaus, 1961; Karageorghis et al., 2009; Pollo, Carlino, & Benedetti, 2008). In addition, the well-documented boost in performance from consumption of glucose is not due to increased availability of glucose to muscles, as studies have shown that orally swishing glucose without ingestion leads to improvements in exercise performance and activation of brain areas associated with reward and motivation (Chambers et al., 2009; Rollo & Williams, 2011). In fact, swishing a glucose solution led to improvements in 1-hour cycling performance, whereas intravenous infusion of glucose did not (Carter, Jeukendrup, & Jones, 2004). It may be that the detection of carbohydrates—not just sweetness—in the oral cavity indicates that there will be additional energetic substrates available (Chambers et al., 2009), thereby altering the fatigue setpoint.

There is evidence that imagined exercises without any actual physical movement or contraction of muscles can increase the strength of a muscle. Participants who imagined performing exercises of a muscle in the left hand every other day for four weeks, but who showed no additional muscle EMG activity during these imagined exercises, demonstrated almost as much increase in maximal voluntary contraction of that muscle as participants who actually performed the same exercises for the same amount of time (Yue & Cole, 1992). Consistent with previous findings, Yue and Cole (1992) found an increase in strength of the hand muscle on the contralateral (untrained) side in both the actual and imagined exercise groups (Hellebrandt Parrish, & Houtz, 1947; Houston, Froese, Valeriote, Green, & Ranney, 1983; Enoka, 1988), suggesting that central nervous system factors play a significant role in determining the maximal force-generating capacity of skeletal muscles.

A “Central Governor” of Physical Fatigue

Based in part on the lack of evidence for the catastrophic failure model of muscle fatigue, Noakes (1997) proposed that there must be a central nervous system mechanism—a central governor—that limits further exertion to prevent homeostatic breakdown. The claim of his “Central Governor Theory” (CGT) is that the brain dynamically and subconsciously modulates the number of active motor units based on a pacing strategy that allows completion of a given task in the most efficient way while maintaining internal homeostasis and a metabolic and physiological reserve (Noakes & Gibson, 2004). The concept of central fatigue, the component of muscle fatigue that is dependent on a progressive failure to voluntarily drive motor neurons and muscle fiber, had existed for some time (Mosso, 1904), as had the claim that maximal voluntary strength is almost never expressed due to central nervous system limitations (e.g., Merton & Pampiglione, 1950). Noakes (1997) was the first to integrate these concepts into a theory based on the principle of homeostasis preservation.

Based on feedback from multiple afferent signals regarding factors such as metabolic rate, fuel reserves, and rate of heat production, a central governor—possibly involving the anterior cingulate—determines subjective feelings of fatigue that increase as the estimated limits of homeostatic stability are approached, ultimately leading to a reduction in motor recruitment and termination of exercise (Noakes et al., 2005; Gibson & Noakes, 2004).

According to CGT, muscle fatigue is not a physical event defined by reduction in muscle force output and caused by peripheral events such as lack of energetic substrate, but rather a subjective feeling analogous to an emotion whose function is to maintain homeostasis and direct behavior to protect the organism (Noakes et al., 2005). In this way, muscle fatigue could be conceptualized as similar to physical pain, a feeling or sensory experience that guides behavior for the purpose of safeguarding homeostasis and organismic integrity (Craig, 2003). This is consistent with Thorndike's idea that "Feelings of fatigue ... serve as a sign to us to stop working long before our actual ability to work has suffered any important decrease" (quoted in Arai, 1912, pp. 72-73).

The Role of Motivation in Physical Fatigue

Were we allowed to regularly expend our energetic resources to the point of depletion or exert our muscles to their full capacity, we would risk physical injury and, without reserve energy for emergency fight-or-flight operations, be left in a position of vulnerability. However, there are clearly times when it would be adaptive to remove or at least modify the limits set by the central governor, such as during life-threatening situations. Therefore, the central governor, like more basic homeostatic mechanisms in the muscles themselves, limits exertion to a degree determined by the conditions. There are documented cases of individuals lifting cars to save trapped victims, a phenomenon referred to as "hysterical strength," such as the man who lifted a 3,000-pound car to free a pinned motorcyclist (Huicochea, 2006). Even taking into account the leverage of lifting only the front of the car from the ground, this amount would be approaching the world record deadlift of 1,008 pounds (Wise, 2009). As predicted by CGT, overriding the central governor can lead to physical injuries, such as torn muscles, ruptured tendons, and broken teeth (Wise, 2010). Such extreme circumstances suggest that it requires a high degree of motivation to override the normal limits of the central governor, though examples of severe injuries during high stakes sports competition and even death during extreme endurance events suggest that committed athletes are also capable of mustering the level of motivation required to override the central governor (Darrow, Collins, Yard, & Comstock, 2009; Matthews et al., 2011; Rowland, 2011).

There are some findings not entirely consistent with CGT, and the theory is not without controversy within the field of exercise physiology. For example, there is some evidence that an exercise-induced buildup of metabolites other than lactic acid, such as hydrogen ions, adenosine diphosphate, or reactive oxygen species, may contribute to a reduction in muscle force output (Allen, Lamb, & Westerblad, 2008; Enoka & Stuart, 1992). Functional electrical stimulation of muscles in spinal cord injury patients eventually results in declines in muscle force and power, suggesting that there may be some limitations of muscle force output at the local level (Jacobs & Mahoney, 2002; Winslow, Jacobs, & Tepavac, 2003). There is also some evidence that the proposed centralized mechanisms of the CGT may not adequately explain the development of fatigue in some exercise situations, such as tasks that require very high forces and/or power outputs for brief periods of time (Weir, Beck, Cramer, & Housh, 2006). However, in the presence of intact neurological pathways, local biochemical changes in the muscles may indirectly lead to muscle fatigue via their feedback to the central nervous system, which in turn leads to reduced muscle recruitment via a

central governor. Despite these and other criticisms of the CGT account of physical fatigue that continue to be debated (e.g., Shephard, 2009), several recent reviews highlight how a central governing mechanism best explains extant knowledge regarding human exercise performance (Noakes, 2012; Shei & Mickleborough, 2013; Loprinzi, Herod, Cardinal, & Noakes, 2013). A central fatigue-governing mechanism such as that proposed in CGT is a helpful framework on which to build a better understanding of self-regulatory fatigue.

Principles of Physical Fatigue Applied to Self-Regulation

Unlike the catastrophic-failure models of muscle fatigue, models that take into account both psychological factors and physiological substrate signals are more consistent with the phenomenology of physical fatigue. Such a perspective can advance our understanding of self-regulatory fatigue beyond the depletion model provided by the SM. Although recent studies supporting the SM acknowledge that psychological factors can temporarily forestall self-regulatory fatigue, they continue to assert that some form of physiological depletion is ultimately responsible for self-regulatory fatigue (e.g., Vohs et al., 2012). Consistent with current models of physical fatigue, it seems that self-regulatory fatigue is due not to a depletion of substrates, but rather a dynamic and integrative governing mechanism in the central nervous system that continuously estimates current work load and energy reserves, anticipated work requirements and energy needs, and goal importance. The output of this complex mechanism affects subjective feelings of fatigue, willingness to continue on a self-regulatory task, or both.¹

For a model of physical fatigue to be applied to self-regulatory fatigue, it must meet the conditions previously laid out. It must account for the following in self-regulatory fatigue: What is known about possible substrates; physiological changes in the entire organism; unusual findings such as the effects of swishing glucose; and the ability of psychological factors such as beliefs and motivation to over-ride self-regulatory fatigue, even when that fatigue is extreme.

With regard to substrates and physiological change, rather than relying on the claim that self-regulatory failure is due to depletion of any particular substrate such as glucose in the blood or in the brain, feedback from various locations and systems in the body may act as signals about the presence or absence of resources that can in turn affect the experience of fatigue. This perspective is consistent with biological science, particularly systems biology in which multiple components simultaneously combine in a complex and dynamic interaction to produce emergent properties in organisms (Noble, 2010). This is in contrast to the reductionist perspective that a complex system can be fully understood by gaining knowledge of its isolated parts (Kitano, 2002). Many types of systems reveal that its patterns are greater than the sum of its parts, such as ant colonies (Sole, Miramontes, & Goodwin, 1993), traffic patterns (Schreckenberg, Schadschneider, Nagel, & Ito, 1995), and psychological constructs such as working memory (Postle, 2006).

¹Some studies suggest that self-regulatory fatigue is not associated with subjective fatigue. A meta-analysis found a significant but heterogeneous effect size of $d = .44$ for subjective fatigue, and a larger effect for perceived difficulty ($d = .94$; Hagger et al., 2010). The heterogeneity in the subjective fatigue effect may reflect measurement differences, as researchers created their own scales or items to measure this construct (Hagger et al., 2010).

With regard to the effects of swishing glucose, a simplistic depletion model cannot account for these findings in exercise endurance or in self-regulatory persistence. The actual level of glucose or any other substrate should not determine the level of fatigue, because it is more adaptive for fatigue to precede and therefore prevent major drops in substrate than to allow levels of any substrate to become depleted before fatigue occurs. Therefore, the extent of fatigue is determined by the expected levels of glucose relative to the estimate of its anticipated need, combined with expected levels and needs of other resources that may be required for successful goal completion. Swishing glucose likely improves self-regulatory endurance because it increases anticipated available resources rather than actually increasing available resources. These effects are probably not specific to glucose; recent evidence suggests that simply handling ibuprofen without ingesting it promotes pain relief, for example (Rutchick & Slepian, 2013).

With regard to the ability of psychological factors such as beliefs and motivation to over-ride self-regulatory fatigue, this may be due to the anticipation of a disturbance in homeostasis, a lack of anticipated benefit for the goal being pursued, or a combination of the two. In contrast to the SM or the glucose depletion hypothesis, in which depletion of an energy source causes self-regulatory failure, a parallel with physical fatigue allows for overcoming fatigue under virtually any circumstances given enough motivation. Vohs and colleagues (2012) found that increasing motivation from baseline prevents fatigue at moderate but not high levels, but the level of motivation in the high fatigue condition was not increased to match the level of self-regulatory fatigue. If motivation were also increased, CGT would predict that individuals could override even high levels of fatigue. This prediction is consistent with everyday examples of what might be called “hysterical self-regulatory strength.” For example, there are documented cases of individuals who continue for days on end to keep both hands on a car without leaning on it or squatting, overcoming even the drive to sleep, in order to be the last person standing and win the car (Bindler, 1997).

Further, fatigue may be directly related to the type of motivation a person has for completing a task. In laboratory studies of self-regulatory fatigue, the motivation for performance on a task is generally extrinsic: An experimenter asks participants to try their best on a task that is irrelevant to the participant. In these cases, even seemingly simple tasks may produce significant fatigue because levels of motivation and perceived benefit are low (Halali, Bereby-Meyer & Meiran, 2014). On the other hand, tasks that are intrinsically motivated may generate less self-regulatory fatigue (Ryan & Deci, 2000). For example, people who reported exercise as fun exhibited less self-regulatory fatigue than others who reported the same exercise as less fun (Werle, Wansink, & Payne, 2014). This suggests that the subjectivity of effort may be related to the motivations people have for completing tasks, with extrinsically motivated tasks—particularly those in which the extrinsic motivation is minimal—being more fatiguing than intrinsically motivated ones.

Summary: Proposed Inputs to Self-Regulatory Fatigue

Subconscious calculations integrate the conceptual, sensory, and contextual aspects of experience in order to make probabilistic predictions about whether and to what extent personal resources should be used. Preliminary evidence suggests that subjective effort

derives from the neural monitoring of performance costs and psychological resources (Tops et al., 2013), providing support for an explanation that suggests that there is a similar process of ongoing subconscious predictions that determine subjective fatigue. It is likely that these predictions are based on Bayesian inference, a method of estimating probabilities that is continually updated as additional evidence or experiences occur (Coan, 2008). These predictions are based on estimates of current conditions (workload, available energy, goal value), expected conditions (future workload and available energy), and opportunity costs of not pursuing some other goal (Proffitt, 2006; Segerstrom & Solberg Nes, 2006; Kurzban et al., 2013). The estimates are continually updated according to a comparison of a representation of the self as tested against incoming sensory information (Craig, 2009). In other words, our expectations about likely outcomes change based on the outcomes of our ongoing experiences. For example, if one were working on a crossword puzzle, the integration of various factors would determine the amount of time and effort one were willing to spend on it before giving up: (1) How much *energy* is available to do this right now? (Baumeister et al., 2007); (2) How much *value* or enjoyment is derived from working on the crossword? (Inzlicht & Schmeichel, 2012); (3) How much *time and effort* did similar crosswords require in the past? (Coan, 2008); (4) What *other tasks* could be worked on instead of the crossword, and what is their value? (Kurzban et al., 2013); (5) What other valued activities might *require energy later*? (Muraven et al., 2006). Since Bayesian inferences are dynamic, the answers to the above questions will change if the crossword starts to take more effort than initially expected, if its value decreases due to a decrease in enjoyment, or if an additional valued opportunity cost appears on the horizon. Importantly, it follows that perceived effort is not only an output of performing self-regulatory tasks, but can serve as an input for future Bayesian calculations on similar tasks (Hennecke & Freund, 2013; Hofmann & Kotabe, 2013). Manipulation of these factors, such as the value of an activity and expected future resource demands, have been shown to moderate self-regulatory persistence (Moller et al., 2006; Muraven et al., 2008; Muraven & Slessareva, 2003). The range of inputs described above demonstrates how a central governor approach to self-regulatory fatigue integrates principles from energy conservation and energy allocation models while also incorporating physiological substrate availability and motivation into a complex feedback system that accounts for fatigue, as well as the ability to overcome fatigue (see Figure 1).

Potential Physiological Mechanisms of Fatigue

There are striking similarities between the proposed central nervous system structures involved in self-regulatory fatigue and those involved in muscle fatigue. Current models suggest that successful regulation—whether it consists of persisting in physical exercise, controlling emotions, or resisting tempting food—is the result of the prefrontal cortex (PFC) exerting adequate neural influence over other brain structures. Research on the neuroscience of self-regulation suggests that the engagement of the PFC is probably necessary for all forms of successful regulation, but the neural structures that must be inhibited are domain specific (Cohen & Lieberman, 2010; Heatherton & Wagner, 2011; Posner, Rothbart, Sheese, & Tang, 2007). For example, when habitual cocaine users inhibit their urges to use cocaine, they show increased PFC activation that is inversely proportional to the decreased activity in

the ventral striatum, an area of the brain associated with appetitive urges (Volkow et al., 2010). Similar activation of the physical PFC-ventral striatum circuit is observed in smokers when cued with cigarettes, and in healthy participants inhibiting urges related to money (Delgado, Schotter, Ozbay, & Phelps, 2008; Kober et al., 2010). In the case of emotion regulation, however, the amygdala rather than the ventral striatum is inhibited (Ochsner & Gross, 2005). For example, in individuals who often fail to regulate their emotions, such as those with mood disorders and high levels of emotional lability, there is decreased connectivity between the PFC and the amygdala (Donegan et al., 2003; Silbersweig et al., 2007; Urry et al., 2006). In fact, recent evidence suggests that individual differences in global connectivity between the physical PFC and other brain areas can be used to predict cognitive control (Cole, Yarkoni, Repovs, Anticevic, & Braver, 2012). It appears that self-regulatory fatigue and failure occur due to either lack of PFC engagement, heightened activity in subcortical structures, or both (Heatherton & Wagner, 2011).

The PFC has also been identified as essential in the successful central regulation of continued muscle recruitment during exercise-induced physical fatigue (for a review, see Tanaka & Watanabe, 2012). Whereas the neuroscience of self-regulation literature emphasizes the inhibition of the amygdala or striatum for successful regulation of emotions or urges, respectively, overcoming muscle fatigue likely requires the PFC to inhibit the anterior cingulate and insula, both of which seem to be activated in proportion to the degree of subjective physical and mental fatigue (Hilty, Jäncke, Luechinger, Boutellier, & Lutz, 2011; Jouanin, Peres, Ducorps, & Renault, 2009; Williamson Fadel, & Mitchell, 2005).

Recent work points to the anterior insula (AI) as an important brain area in the monitoring of afferent inputs, and suggests that any central governing mechanism would likely have functional connectivity with the AI. The AI is thought to generate interoceptive “gut feelings” such as whether or not someone is trustworthy (Castle et al., 2012), but evidence suggests that the AI may also be involved in monitoring and regulating peripheral resources including muscle condition, aversive body states, blood glucose levels, and autonomic activation (Tops, Bokse, & Koole, 2013). Interoceptive feelings generated in the AI may produce the experience of fatigue, which serves as a valuation of energy utilization and may thereby promote a homeostatic sensorimotor template (Craig, 2013).

Afferent inputs from the periphery that inform the central governor likely include levels of blood glucose and muscle glycogen, blood acid and muscle acid, ergoreceptors in skeletal muscle, blood oxygen levels, lipid stores, liver glycogen stores, cortisol levels, cardiovascular state, immune system activity, and thermal conditions of the body (Gandevia, 2001). The central governor may be particularly sensitive to heat based on the evidence that subjective fatigue, exercise exhaustion, and self-regulatory performance are all affected by heat: Higher ambient temperatures are associated with increased aggression (Kenrick & MacFarlane, 1986; Reifman, Larrick, & Fein, 1991; for a review, see Anderson, 2001), reduced persistence on physical tasks (Galloway & Maughan, 1997; Meeuseen, Watson, & Dvorak, 2006; Nielsen, Hyldig, Bidstrup, Gonzalez-Alonso, & Christoffersen, 2001; Nielsen & Nybo, 2003; Parkin et al., 1999), and impaired attentional control (Bhattacharya, Tripathi, Pradhan, & Kashyap, 1990; Hancock, 1982; Lieberman et al., 2005), all of which are indicative of self-regulatory impairment. Some information, such as level of muscle

recruitment, is transmitted through the spinal cord to the thalamus, a kind of relay station for sensory and motor signals from the periphery to the cerebral cortex (Tanaka & Watanabe, 2012). However, other signals to the brain likely travel a different route. The vagus nerve, which consists of 80-90% afferent fibers, carries a vast amount of information from the body to the brain, including the state of the heart, lungs, gut, and immune system (Berthoud & Neuhuber, 2000; Grundy, 2002). Therefore, the afferent vagus is in an excellent position to inform the central governor about a number of important aspects of the body, such as nutrient availability, infections in the body, and cardiorespiratory state.

Why Do We Experience Self-regulatory Fatigue?

One important difference between physical fatigue and self-regulatory fatigue is the ultimate function of the governing mechanism. Physical fatigue serves the purpose of maintaining homeostasis and protecting the organism from physical damage, but it is less clear what the purpose of self-regulatory fatigue is, or why we need a central governor in self-regulation. There are documented cases of physical damage resulting from overriding the central governor, such as tissue damage (Kim, Lee, & Kim, 2007; Neilan et al., 2006), but there is no evidence of neurological damage having ever occurred due to prolonged or intense bouts of self-regulation. The only circumstances under which such damaging levels of activity in the central nervous system occur is during a seizure (Sutula, Hagen, & Pitkanen, 2003), which produces a level of activity in the brain that is surely greater than that generated by even the most intense levels of self-regulation. Although the primary purpose of this review is to consider the number and nature of *inputs* that determine self-regulatory fatigue as informed by knowledge about physical fatigue, insofar as purely physiological and purely psychological explanations for the mere existence of self-regulatory fatigue have to date proven unsatisfactory (see above), two possibilities are offered below.

First, physical fatigue and self-regulatory fatigue may not be separate systems. Self-regulatory fatigue may have coopted or appropriated the pre-existing neural machinery of the central governor to promote the maintenance of homeostasis. An example of cooptation (or exaptation) is the way the stress response is speculated to have appropriated for its own purposes the machinery of the immune system (Maier, Watkins, & Fleshner, 1994). As an evolutionarily old system, the innate immune system already had mechanisms for mobilizing in case of infection (i.e., the inflammatory response). As the stress response later developed as a tool for managing predators and other dangers, including the infection risk associated with these dangers, the machinery of the innate immune system turned to this purpose (Maier et al., 1994). Considering that self-regulatory fatigue has been observed in dogs as well as humans (Miller et al., 2010), it is likely that the overlap between physical fatigue and self-regulatory fatigue is common to other mammals and occurred relatively early in evolutionary history.

Crossover fatigue effects for acts of mental and physical self-regulation suggest overlapping systems. Performing a mentally demanding task, such as focusing one's attention on a video of a person's face while ignoring words scrolling at the bottom of the screen, produces regulatory fatigue on a subsequent physical self-regulation task, such as tightening a handgrip for as long as possible (Muraven et al., 1998). Mental fatigue has also been shown

to reduce physical endurance, despite no resources being depleted at the local muscle level (Pageauk et al., 2013). Likewise, inhibiting physical movement during a boring task leads to reduced inhibition of aggression in response to an insult (Stucke & Baumeister, 2006).

One possible exception to the general rule of a crossover fatigue effect is that some research suggests that executive functioning tasks such as inhibition show improvement following moderate or intense bouts of aerobic exercise (for a review, see Tomporowski, 2003). However, the evidence for this effect is mixed, and recent studies show no change or a decline in executive functioning as a result of an acute bout of aerobic exercise (Labelle, Bosquet, Mekary, & Bherer 2013; Coles & Tomporowski, 2008). Furthermore, several of the studies showing declines used 5 – 10 minute rest periods following exercise termination, so the recovery period could allow for a return to baseline functioning (e.g., Heckler & Croce, 1992). Finally, there is evidence that brief bouts of aerobic exercise function as a central nervous stimulant, similar to caffeine, which may offset what would otherwise be a decline in self-regulatory capacity due to physical exertion (Tomporowski, 2003).

One evolutionary advantage of the self-regulatory fatigue system coopting the physical fatigue system is conservation of energy, even if the energetic savings are small. The body is motivated toward being energetically conservative as set forth in the biological principles of “least effort” (Gendolla & Richter, 2013). All organisms operate according to certain biological principles, one of which is economy of action: Energy consumption must exceed energy expenditure (Kacelnik & Cuthill, 1990; Davies, Krebs, & West, 2012; Proffitt, 2006). As noted above, energetic conservation characterizes episodes of self-regulatory effort, which have a quiescent effect on the cardiovascular and immune systems, as well as other visceral organs (Eisenlohr-Moul et al., 2012; Segerstrom, 2007, 2010; Segerstrom & Solberg Nes, 2007). This physiological set is also consistent with the finding that subjects avoid cognitive demand and hold back or reduce regulatory effort when they are told to expect future self-regulatory tasks (Kool, McGuire, Rosen, & Botvinick, 2010; Muraven et al., 2006; Tyler & Burns, 2008). Even human sensory perception is modified in ways that bias decision-making to manage energy use efficiently (Proffitt, 2006). For example, wearing a heavy backpack makes distances seem further away, and uphill inclines seem steeper (Stefanucci, Proffitt, Banton, & Epstein, 2005). Additionally, under conditions of self-regulatory fatigue, people endorse statements that rationalize inaction or less effortful goal pursuit (van Dellen, Shea, Davisson, Koval, & Fitzsimons, 2014). Although the energetic demands of self-regulation are minimal (Beedie & Lane, 2011; Clarke and Sokoloff, 1998), the brain is inarguably an organ like the muscles and heart. As is true for other organs, its energetic use may be an input (but not the only input) to the experience of fatigue. As is also true for other organs, it is possible for the experience of fatigue to be out of proportion to the actual energy requirements of the organ relative to the amount of substrate available.

Although this explanation cannot be definitively ruled out at this point, it is thought to be unlikely and is entirely unsatisfactory on one point: Fatigue is specific to self-regulation. A purely energetic conservation explanation seems inconsistent with the findings that fatigue is observed in the sequential-task paradigm but not following cognitively effortful (and presumably energetically taxing) tasks that do not involve self-regulation. Another possibility is that overriding dominant responses in the short term may be adaptive insofar as

it allows for flexibility in responding, but overriding dominant responses for prolonged periods of time might entail suppression of evolved drives and behaviors associated with survival and reproduction. Therefore, self-regulatory fatigue might have evolutionary value, whereas fatigue in other kinds of cognitive effort might not.

As in the adaptive value of emotions, our naturally dominant responses are likely those that succeeded in preserving our ancestors in the past, even though they may sometimes lead us astray in the modern world (Baumeister et al., 1994). Drives such as fear and hunger are evolutionarily adaptive precisely because they promote fleeing from predators and the intake of nutrients, and therefore have high value for survival and reproduction. Temporarily overriding dominant responses offers flexibility of responding, but overriding basic drives, such as those for food and sex, or suppressing an emotion such as fear, is more maladaptive the longer it occurs. It has also been argued that there are significant affective, cognitive, behavioral, and physical health costs to chronically inhibiting impulses (Polivy, 1998). For example, those who chronically inhibit the urge to eat food for the purpose of losing weight tend to experience higher levels of negative affect and are more distractible than those who are not restraining (Herman & Polivy, 1988), may have higher rates of adverse health events than those of similar weight who are not restraining (Wooley & Wooley, 1984), and tend to engage in excessive displays of the initially inhibited behavior in the form of binge eating (Polivy & Herman, 1987). Anorexia nervosa, an extreme case of chronic inhibition of the drive to eat, can result in damage to almost every major organ system in the body, and sometimes death (Arcelus, Mitchell, Wales, & Nielsen, 2011).

Evidence reveals that self-regulatory fatigue enhances the neural responses to rewards and impairs top-down control, thereby decreasing the likelihood of always being regulated (Wagner, Altman, Boswell, Kelley, & Heatherton, 2013). The qualities of self-regulatory fatigue—increasing the longer it is used, but rather quickly restored—make it more likely that self-regulation will be deployed episodically and not chronically. Thus, one can override dominant responses when appropriate, but the experience of fatigue and reemergence of the dominant response may have also served to increase evolutionary fitness.

Fatigue: Future Directions

The SM and the glucose depletion hypothesis, motivation models, motivation/attention models, and opportunity cost models have all generated concrete and testable hypotheses. A model based on parallels with physical fatigue is broader than these theories in that it includes a number of motivational and physiological inputs as necessary for the experience of self-regulatory fatigue. Importantly, there are factors associated with physical fatigue that have not been tested with regard to self-regulatory fatigue. If self-regulatory fatigue and physical fatigue are close cousins (if not the same phenomenon) as is argued in this paper, then the same factors should affect both self-regulatory fatigue and physical fatigue. This has been true for many factors, but further tests of this hypothesis are possible.

Considering the proposed overlap in neural structures responsible for physical and mental fatigue, individuals who are more sensitive to one kind of fatigue should be more sensitive to the other. Participants' sensitivity to exercise-induced fatigue could be compared to their

sensitivity to self-regulatory fatigue to test for the expected strong positive correlation between the two. Those who are particularly vigilant for signs or symptoms of physical fatigue should also be vigilant for signs and symptoms of self-regulatory fatigue. This could be examined using the vicarious depletion paradigm described earlier in which participants are shown videos of others appearing physically or mentally exhausted (Ackerman et al., 2009).

Factors that increase or decrease one type of fatigue should increase or decrease the other. For example, higher ambient temperatures have been shown to negatively impact exercise endurance and self-regulatory performance, yet this could be further examined using a within-subjects design to test whether intra-individual body temperature fluctuations correlate with subjective fatigue and performance on self-regulatory and endurance exercise tasks. There is evidence that caffeine and sodium bicarbonate can enhance aerobic exercise endurance (Dunford & Smith, 2006; Gandevia & Taylor, 2006), but the ability of these and other ergogenic aids to affect self-regulatory fatigue remains largely untested. Recent evidence finds that Ritalin, a stimulant, helps prevent self-regulatory fatigue (Sripada, Kessler, & Jonides, 2014). Conversely, some forms of ginseng extract may reduce subjective mental fatigue and improve executive functioning performance (Reay, Kennedy, & Scholey, 2005; Scholey et al., 2010), but ginseng's ability to counteract exercise-induced physical fatigue has not been tested (for a review, see Bahrke & Morgan, 2000). To the extent that there are manipulations or substances that have a significant effect on self-regulatory fatigue without a concomitant effect on physical fatigue, or vice versa, this would argue against a unified model of physical and mental fatigue.

Other afferent physiological inputs may influence the experience of self-regulatory fatigue. Biochemical signals suggesting increases in energy demand are likely to promote more rapid self-regulatory fatigue, in the same sense that signals suggesting increases in energy supply (e.g., glucose in the oral cavity) protect against self-regulatory fatigue. For example, the immune system can be as energetically expensive as other organs such as the brain and heart. When activated, the immune system produces proteins (cytokines; e.g., interleukin-1) that affect the central nervous system via the vagus nerve, producing sickness behavior, an adaptive response designed to conserve energy so that the immune system can mount an effective response. Sickness behavior includes motivational changes such as lethargy and reduced appetite and sex drive. It is likely that these motivational changes are designed in part to reduce energy and substrate use by other parts of the body (e.g., skeletal muscle) and make those resources available to meet the energetic demands of an activated immune system (Aubert, 2012; Maier et al., 1994; Segerstrom, 2010; Straub, 2012). Therefore, these "sickness" cytokines should result in decrements in both self-regulatory and exercise endurance.

Although previous studies have examined the effects of an acute bout of aerobic exercise on some tasks of executive functioning, the methodological variation in these studies, including rest periods between the exercise bout and executive functioning task, makes it difficult to reach any conclusions in this area. Because we argue that physical and self-regulatory fatigue have significant overlap in neural structures, we expect that the duration and intensity of an initial bout of aerobic exercise would be inversely related to performance on an

immediately proceeding self-regulatory task. Functional magnetic resonance imaging scans could be helpful in examining whether similar brain areas are activated during both types of tasks, particularly when performed sequentially.

There are a number of potentially important implications of a model of self-regulatory fatigue that draws on models of physical fatigue. Future self-regulation research should include measurement of physiological and psychological variables because both can affect level of self-regulatory fatigue. If fatigue is influenced by multiple physiological and psychological inputs, there may also be greater avenues for altering the experience of fatigue than would be expected in substrate-based or cognitive-based models of self-regulation. For example, large enough motivational rewards may be sufficient to override even significant physiological inputs that tend to increase fatigue, such as chronic physical disease (e.g., fibromyalgia; Solberg Nes, Carlson, Crofford, de Leeuw, & Segerstrom, 2010). This speaks to a broader question for future research regarding the relative weighting of these inputs. Under some circumstances and for some people, motivational inputs may have greater influence than physiological inputs. It seems likely that for healthy younger people participating in laboratory-based experiments who comprise the majority of extant self-regulatory research, motivational inputs play a larger role than physiological ones. In addition to examining the quantity and quality of motivation, it will be important to measure and explore the relationships between subjective fatigue, self-regulatory failure, and resource availability, as a central governor approach suggests that these three factors can dissociate from each other. Finally, if self-regulatory fatigue functions like an emotion, it could be fruitful to examine the extent to which emotion regulation techniques such as cognitive reappraisal are effective for managing self-regulatory fatigue.

Summary and Conclusion

The SM has accrued an impressive record of predicting when individuals are more likely to become fatigued and falter at self-regulation, but the strict limited-resources explanation for why this occurs is inconsistent with a variety of behavioral and physiological evidence. Alternative models that posit a purely motivational or cognitive account of self-regulatory fatigue underemphasize the important role played by homeostatic mechanisms. The motivational and physiological models are both partially right, but a fuller explanation of the causes of self-regulatory fatigue needs to integrate the two.

Drawing on what is known about physical fatigue allows for the generation of novel hypotheses regarding the causes, consequences, and correlates of self-regulatory fatigue and self-regulatory failure. Only by adopting an integrative account of self-regulatory fatigue can researchers begin to understand the contributions of specific physiological substrates, mental processes, and their interactions. A shared framework for self-regulatory and physical fatigue has important implications for a wide number of disciplines beyond psychology, including exercise science, physical therapy, and medicine.

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Figure 1. Model of self-regulatory fatigue informed by Central Governor Theory