

Motivation and Cognitive Control: From Behavior to Neural Mechanism

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Abstract

Research on cognitive control and executive function has long recognized the relevance of motivational factors. Recently, however, the topic has come increasingly to center stage, with a surge of new studies examining the interface of motivation and cognitive control. In the present article we survey research situated at this interface, considering work from cognitive and social psychology and behavioral economics, but with a particular focus on neuroscience research. We organize existing findings into three core areas, considering them in the light of currently vying theoretical perspectives. Based on the accumulated evidence, we advocate for a view of control function that treats it as a domain of reward-based decision making. More broadly, we argue that neuroscientific evidence plays a critical role in understanding the mechanisms by which motivation and cognitive control interact. Opportunities for further cross-fertilization between behavioral and neuroscientific research are highlighted.

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INTRODUCTION

Concentration comes out of a combination of confidence and hunger.

—Arnold Palmer

Cognitive control:

the set of superordinate cognitive functions that encode and maintain a representation of the current task, marshaling to the task subordinate functions including working, semantic, and episodic memory; perceptual attention; and action selection and inhibition

Motivation:

the orienting and invigorating impact, on both behavior and cognition, of prospective reward

Picture an undergraduate student sitting in the library with the intention of studying for an exam. Sometimes she finds it’s going well. She is able to attend closely to the material and to devise and execute effective strategies for retaining it. At other junctures, she struggles to concentrate, feeling drawn to her email or social network accounts. Sometimes she yields to these impulses, feeling she really needs a rest. At others, she reapplies herself, compelled by the thought that if she doesn’t, the exam might not go well, undermining her hopes of gaining admission to a prestigious medical school.

From a psychological point of view, this scenario centers on cognitive or executive control, the set of functions that regulate more basic attention-, memory-, language-, and action-related faculties and coordinate their activity in the service of specific tasks. In this regard, the cognitive processes underlying the student’s experience are relatively well understood; executive or cognitive control has been a core research topic in cognitive science essentially since the field’s inception (Miller et al. 1960, Posner & Snyder 1975). Several decades of research have established key behavioral phenomena (Banich 2009), revealed some basic computational (Botvinick & Cohen 2014, O’Reilly et al. 2010) and neural mechanisms (Mars et al. 2011, Miller & Cohen 2001), and elucidated the nature and origins of individual differences in control function (Miyake & Friedman 2012).

However, there is also a side to the library vignette that we do not yet understand quite so well. This involves the aspects of the scenario that relate to the interaction of cognitive control and motivation. It is clear that the student in the story is mobilizing cognitive control for a reason,

and that this reason has directly to do with desired outcomes that can be brought about by the application of control, as well as with undesired outcomes that would follow from a failure to apply control. Furthermore, when the student has difficulty concentrating on her coursework, this seems likely to occur because at some level she does not actually *want* to concentrate. Although it may be necessary to review for the exam, it is not inherently enjoyable. In short, the function of control is driven, powerfully and fundamentally, by the student's desires and goals. Control is motivated.

Once it is acknowledged that motivation may play an important role in cognitive control, a number of important questions arise, many of which go beyond those that have traditionally guided control research. What exactly are the motivational factors that fuel executive function? Via what mechanism (or mechanisms) do incentives trigger control to engage, to withdraw, to shift focus? What role might motivation play in driving the temporal dynamics of control, its tendency to vary in focus and intensity over time? Obviously, these are questions that, in addition to their academic relevance, also have a direct bearing on practical matters, including education, workplace performance, and a range of clinical disorders, ranging from chronic fatigue syndrome to attention-deficit/hyperactivity disorder (ADHD) to addiction.

In recognition of these points, recent research on cognitive control has increasingly focused on its interaction with motivation. This reorientation has triggered new developments across a diverse set of fields, including cognitive psychology, computational reinforcement learning, social cognition, and behavioral economics. One aim of the present review is to provide a selective overview of the key empirical observations and theoretical assertions that have emerged from these collected disciplines to date.

Our primary objective, however, is to consider the relations between those findings and observations from yet another domain of research: neuroscience. Like behavioral research, neuroscientific research on cognitive control has also recently become increasingly focused on issues of motivation. It is tempting to see such neuroscientific work as constituting a special topic, a source of information that can be safely ignored if one is exclusively interested in behavior. In particular, the temptation is to view neuroscientific research in this (and other) areas as involving a search for the neural correlates of processes that can be fully specified and understood without reference to the brain. Although this attitude may conceivably be defensible in some domains, we argue that it is misguided when it comes to the interface of motivation and control. Far from being a special topic, neuroscience lies squarely on the critical path toward truly understanding the motivation-control link, holding an indispensable key to settling core issues. With this in mind, our overarching aim in the present work is to contribute toward the dismantlement of the walls that currently tend to segregate neuroscientific work on motivation and control from psychologically and behaviorally focused investigations.

Scope and Definitions

The terms “cognitive control” and “motivation” can take on different meanings in different research contexts, and so it behooves us to provide an explicit definition for each of these terms. By cognitive control, we refer to that set of superordinate functions that encode and maintain a representation of the current task—i.e., contextually relevant stimulus-response associations, action-outcome contingencies, and target states or goals—marshaling to that task subordinate functions including working, semantic, and episodic memory; perceptual attention; and action selection and inhibition. The state of control at any instant can be characterized in terms of (*a*) its direction, the specific task objectives toward which control is directing subordinate systems;

Incentive: a value- or reward-laden outcome that is associated by a decision maker with a particular line of behavior and that is assumed to motivate that behavior. The value in question can be positive or negative, and the incentive itself can be intrinsic to behavior itself, as when the decision maker finds performance of a task inherently enjoyable

INDIVIDUAL AND GROUP DIFFERENCES

The impact of motivation on control function has been shown to vary in systematic ways across individuals both with (a) the baseline inclination to engage in controlled information processing (see Westbrook et al. 2013) and (b) general sensitivities to reward and punishment (see Braem et al. 2012, 2013; Engelmann et al. 2009; Fröber & Dreisbach 2014; Jimura et al. 2010; Locke & Braver 2008; Padmala & Pessoa 2011; Savine et al. 2010). On the neural level, behavioral reward sensitivity positively predicts responses to incentives during cognitive tasks in reward and control networks (Engelmann et al. 2009, Jimura et al. 2010, Locke & Braver 2008, Padmala & Pessoa 2011) as well as in functional connectivity between these networks (Padmala & Pessoa 2011). Interestingly, elevated sensitivity to incentives, at both behavioral and neural levels, appears to arise during adolescence (Geier et al. 2010, Jazbec et al. 2006, Luciana & Collins 2012, Luna et al. 2013, Padmanabhan et al. 2011, Somerville & Casey 2010, Somerville et al. 2011), one of numerous examples of the moderation of motivation and control interactions by age (Ennis et al. 2013, Somerville & Casey 2010, Westbrook et al. 2013) and/or clinical profile (Barch et al. 2008, Slusarek et al. 2001, Strand et al. 2012, Strauss et al. 2013, Treadway et al. 2012).

and (b) its intensity, the strength of its top-down input to those systems (Bonner & Sprinkle 2002, Shenhav et al. 2013).

By motivation, in turn, we refer to the orienting and invigorating impact, on both behavior and cognition, of prospective reward (both extrinsic reward such as money and intrinsic reward tied to the satisfaction of self-relevant behavioral goals, and including negative rewards, i.e., punishments). The study of motivation also often includes a focus on specific motivational content, that is, the particular behavioral goals to which people tend to strive or the specific outcomes or activities that they find rewarding or reinforcing.

These definitions put us in position to be more precise about the scope of the present review. In particular, we aim to review empirical findings and theories relating to cases where motivational context impacts the intensity or direction of control. A number of topics, though undoubtedly related to the topic so stated, must fall outside the scope of our review, given limited space. These include effects relating to mood or affect (Chiew & Braver 2011, Pessoa 2008, van Steenbergen et al. 2012); effects of subliminal incentive cues (Bijleveld et al. 2009, Zedelius et al. 2014); the impact of control on motivation itself, as seen in the setting of self-control (Hare & Rangel 2009, Wagner et al. 2013); individual differences related to stable personality traits (Braem et al. 2013, Jimura et al. 2010); and changes associated with development, aging (Ennis et al. 2013, Mather & Carstensen 2005), and various clinical disorders, such as ADHD and schizophrenia (Marx et al. 2013, Strauss et al. 2013) (see sidebar Individual and Group Differences).

The remainder of the review is organized as follows. We begin, in the following section, by briefly introducing a core set of behavioral observations relating to motivation and cognitive control. We then compare and contrast the set of theoretical perspectives that have dominated interpretations of these core observations, arguing here for the important role of neuroscience. Next, we turn to a review of the neuroscience literature on motivation and control interactions, and we close with a set of broader observations concerning the potential synergy between neuroscientific and behavioral research.

CORE BEHAVIORAL PHENOMENA

Here we briefly highlight a set of key behavioral phenomena relating to the interface between motivation and control. These can be organized under three headings, which we consider in turn:

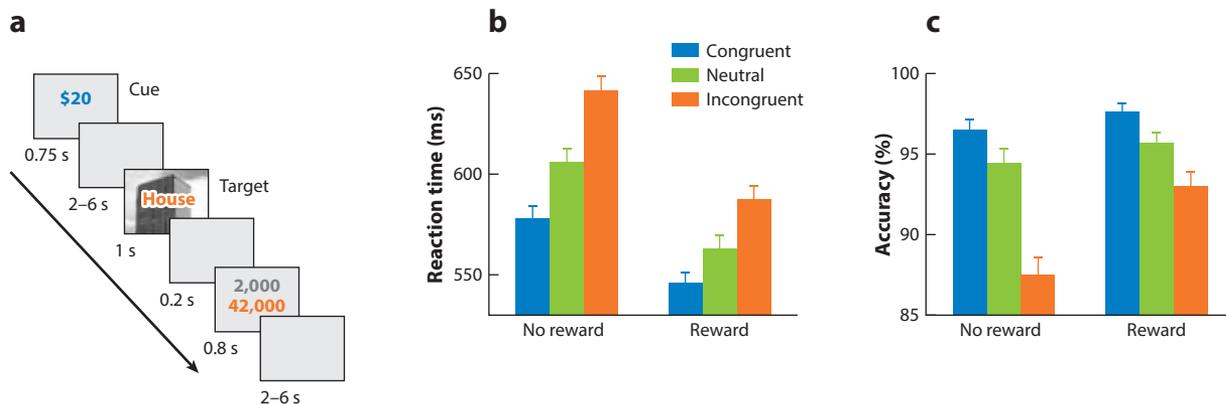


Figure 1

The results of a selective attention task indicate that incentives enhance cognitive control. (a) Illustration of the conflict task used by Padmala & Pessoa (2011). In a reward condition (shown here), an initial cue (\$20) indicated that participants would be rewarded for fast and correct performance. In another condition (not shown), the initial cue (\$00) signaled that no reward was available. Following a short delay, a stimulus containing a picture of a house or building was shown along with a task-irrelevant word. Subsequent to the subject's response, the screen displayed the potential reward and total number of points accrued. (b) Mean reaction times from reward and no-reward conditions in three stimulus conditions. (c) Mean response accuracy. Adapted with permission from Padmala & Pessoa (2011).

(a) the impact of incentives on control function, (b) the role of motivational factors in the temporal dynamics of control, and (c) the inherent cost of cognitive control.

The Relationship Between Incentives and Performance

Perhaps the most fundamental set of phenomena linking control with motivation involves effects of incentives on the performance of cognitive tasks. The most common observation in this arena is simple: The introduction or enlargement of performance-contingent rewards or punishments results in improvements in task performance, specifically attributable to enhanced executive control.

An illustrative example comes from Padmala & Pessoa (2011) (Figure 1). This study involved a Stroop-like selective attention task, in which participants were to classify a presented image as a building or house while ignoring an overlying incongruent, neutral, or congruent letter string (*HOUSE*, *BLDNG*, or *XXXXX*). Critically, some trials began with a trial precue that indicated an available monetary reward for fast, correct responses, whereas other trials offered no reward. Enhanced performance was found on reward trials relative to nonreward trials, in terms of both error rates and response times. More specifically, not only were interference effects (i.e., on incongruent distractor trials) smaller on reward trials, but so also were facilitation effects (i.e., on congruent distractor trials). This latter finding indicates a relatively selective effect in attenuating the influence of the irrelevant distractor on attention and responding. In other words, incentives appeared to enhance cognitive control.

Similar incentive-induced performance improvements in control have been observed in a range of other tasks, tapping other facets of executive function. Libby & Lipe (1992), for example, reported improvements in a free recall task when participants were paid per correct item, reflecting enhancements in the control of episodic memory encoding and retrieval (see also Adcock et al. 2006, Wittmann et al. 2005). Leotti & Wager (2010) observed improvements in a stop-signal task, reflecting enhancements in response inhibition (see also Boehler et al. 2014, Padmala &

Pessoa 2010). Comparable incentive-induced performance enhancements have been observed in task switching (Aarts et al. 2010, Kleinsorge & Rinkebauer 2012, Nieuwenhuis & Monsell 2002), working memory (Gilbert & Fiez 2004, Heitz et al. 2008, Jimura et al. 2010, Taylor et al. 2004), context processing (Chiew & Braver 2013, Locke & Braver 2008), and visual search (Navalpakkam et al. 2009).

Although all of these studies have observed enhancements in control with increasing incentives, it is important to note that this relationship is not inviolable. The broader literature, and in particular research in behavioral economics, has revealed a number of boundary conditions, beyond which incentives may have little effect on cognitive performance and can even undermine it. First, perhaps obviously, incentives are liable to trigger performance improvements primarily in task settings where adjustments in the intensity or direction of control tend to be efficacious (Camerer & Hogarth 1999). This excludes settings where task complexity outstrips the subject's skill set (Bonner et al. 2000, Rydval 2011) or basic information-processing capacity (Awasthi & Pratt 1990, Rydval & Ortmann 2004). Second, paradoxical effects can arise when incentive magnitude becomes either very small or very large. Small monetary rewards can undermine performance, relative to no pay, if the payments are so small as to appear insulting (Gneezy & Rustichini 2000), and very large performance incentives can sometimes induce decrements in performance, a phenomenon sometimes referred to as "choking under pressure" (Ariely et al. 2009, Baumeister 1984, Beilock 2011, Bonner et al. 2000, Camerer & Hogarth 1999, Mobbs et al. 2009, Samuels & Whitecotton 2011, Worthy et al. 2009, Zedelius et al. 2011). Finally, although a wealth of research shows that the investment of cognitive effort can be driven by internal sources of motivation (e.g., need for cognition or achievement motivation; Cacioppo et al. 1996, Deci & Ryan 2000, Nicholls 1984, Satterthwaite et al. 2012), some research has suggested the existence of an undermining effect, according to which the introduction of extrinsic (e.g., monetary) rewards can reduce the intrinsic motivation associated with a task (see Murayama et al. 2010).

Although such findings indicate that the relationship between incentives and control may not be entirely straightforward, they nonetheless combine with the observations described previously to show that the relationship is generally extremely strong.

The Dynamics of Control

Another set of key observations at the interface of motivation and cognitive control relates to the temporal dynamics of control. In almost any task context, the intensity and direction of control tend to vary over time, both in response to the details of the task and independent of them (Eichele et al. 2008, Esterman et al. 2013, Weissman et al. 2006). Such fluctuations have been observed to occur at both short and long timescales, and in both cases the relevant phenomena are tightly connected with motivation.

On a short, trial-to-trial timescale, control is known to vary in response to ongoing performance monitoring. One hallmark of such monitoring is an increase in reaction time on trials following errors. Stürmer et al. (2011) observed an increase in such error adaptation in the context of performance-contingent reward (see also Boksem et al. 2006). In the case of conflict monitoring, a standard observation is that responses associated with high conflict tend to be followed by performance reflecting an increased focus on task-relevant information or a shift toward a more conservative response threshold. Conflict adjustment effects have also been observed to increase in size following performance-contingent monetary rewards (Braem et al. 2012, Stürmer et al. 2011) as well as following performance-contingent punishments (losses) (Braem et al. 2013; for review, see Dreisbach & Fischer 2012). One further connection between conflict and motivation is the proposal that conflict may act as an aversive signal prompting task avoidance (Botvinick

2007). Consistent with this, Lynn et al. (2012) found that experimental participants performing Stroop and working-memory tasks reported an increase in the urge to quit immediately following difficult, conflict-inducing trials.

Different effects linking control and motivation are seen at longer timescales. A key set of findings arising from the social/personality literature, under the heading of the ego depletion effect (for review, see Hagger et al. 2010), suggests that engagement in a control-demanding activity is followed by reduced persistence and/or poorer performance on a second task, compared to when that second task is preceded by a less demanding activity. Initial demonstrations focused on a range of self-regulatory behaviors, such as following a diet, solving an anagram, and suppressing emotional responses (Muraven & Baumeister 2000). More recent work has suggested that such phenomena are present in standard experimental paradigms of cognitive control as well. For example, in a study by Schmeichel (2007) two groups of participants first watched a video clip, one under attention-distraction conditions (ignoring words shown at the bottom of the screen) and the other not. Both groups then performed the same standard test of working memory span. The attention-distraction group showed a subsequent reduction in measured working memory capacity, relative to the control group. Similar findings were observed across a range of studies using different cognitive control tasks (for both the first and second phase).

Traditionally, these types of depletion effects have been explained in terms of a structural constraint on the capacity for sustained cognitive control, manifesting as a kind of refractory period following the control exertion (Baumeister et al. 1998). However, recent work has adopted an alternative perspective on the depletion effect, characterizing it as a motivational phenomenon. Specifically, Inzlicht and colleagues (2014) have proposed that “self-control exertion at Time 1 leads to the motivated switching of task priorities, wherein mental work becomes increasingly aversive, making mental leisure increasingly attractive” (p. 130; see also Inzlicht & Schmeichel 2012). This possibility is supported by a number of studies demonstrating that depletion can be reduced or eliminated by performance incentives (e.g., Boksem et al. 2006, Inzlicht et al. 2014, Muraven & Slessareva 2003).

The Cost of Control

The idea that cognitive control may be inherently costly or aversive has cropped up not only in the depletion literature but also in connection with other topics in social cognition (Taylor 1981) and behavioral economics (Bonner & Sprinkle 2002, Smith & Walker 1993, Wilcox 1993). In such contexts, the cost of control has generally been introduced as an explanatory principle, serving to account for other phenomena (e.g., problem-solving strategies or patterns of social judgment; for review, see Kool et al. 2010). It has not been until recently that control costs have been postulated as measurable phenomena in and of themselves and subjected to direct empirical test.

To this end, Kool and colleagues (2010) introduced a demand-selection paradigm, in which participants chose repeatedly between two sources of task stimuli that demanded subtly different levels of cognitive control. Across a number of task variations, Kool et al. (2010) observed a consistent preference for the lower-demand source (see also Schouppe et al. 2014). Detailed behavioral analyses confirmed that this preference was not wholly driven by error avoidance or by minimization of time on task. Similarly, Westbrook et al. (2013) gained evidence for a cost of control using an economic discounting paradigm. Here, participants were presented with a series of choices between performing a low-demand task at a particular level of pay and performing a more demanding task for a different wage. The payment offered for the high-demand task was titrated until an indifference point was identified. Invariably, this indifference point occurred at a point where the pay offered for the high-demand task was substantially higher than that for

Ego depletion: reduced performance on a cognitive task when that task is performed after another cognitively demanding activity. The term derives from a theory attributing the effect to depletion of a metabolic resource

the low-demand task, suggesting that participants had economically discounted the value of the high-demand task (for related findings, see Dixon & Christoff 2012).

Cognitive energetics theory (CET): a model that draws heavily on a force-field metaphor to account for the impact of motivation on cognitive control

THREE THEORETICAL PERSPECTIVES

As is evident even from the brief overview we have just provided, the relationship between motivation and cognitive control has been considered in a strikingly diverse range of subfields of behavioral research, including cognitive psychology, social and personality psychology, behavioral economics, and research on both self-control and behavioral energetics.

Cutting across these fields, one finds three basic theoretical approaches to the relationship between motivation and cognitive control. One utilizes a force-field metaphor. A second centers on the notion of a limited-capacity resource. The third views the topic in terms of reward-based decision making. Before entering into our review of the neuroscience literature—and to prepare the ground for it—we consider these three theoretical approaches, weighing up their relative strengths and weaknesses.

Force-Field Models

The use of force-field metaphors has been commonplace in motivational research since the time of William James, with their influence strongly bolstered by the work of Kurt Lewin (see Atkinson & Birch 1978) as well as by accounts inspired by physiology, such as drive theory (Berridge 2004, Hull 1943, Miller 1951). The basic idea is to conceptualize action as the result of forces, akin to physical forces, that attract an individual toward a goal or else impede progress toward that goal. Action choice is then explained through an analysis of these driving forces and their interplay.

Carrying this tradition forward, some investigators have applied the force-field metaphor to the problem of motivation in cognitive control. A recent and highly developed example of this approach, arising from the social/personality perspective, is cognitive energetics theory (CET), put forth by Kruglanski and colleagues (2012) (**Figure 2a**). Here, the energy invested in a cognitive activity is determined by an effective driving force. This, in turn, is a function of two other quantities: (*a*) a potential driving force that scales with both goal importance and a pool of available mental resources, which sets an upper bound on the effective driving force; and (*b*) an opposing restraining force, that is modulated both by task difficulty and by the individual's inclination to conserve resources. According to CET, the effective driving force rises to the level of the restraining force, subject to a limit imposed by the potential driving force. Kruglanski and colleagues (2012) apply this force-field model to a wide variety of phenomena ranging from biases in judgment to incentive effects under fatigue.

Resource Models

The CET model reviewed above involves, as one of its ingredients, the idea that cognitive activity consumes some form of resource and that the available quantity of this resource imposes a limit on cognitive processing. This notion of a limited resource figures in a wide range of theories addressing the relationship between motivation and cognitive control (see, e.g., Bijleveld et al. 2009, Persson et al. 2013, Pessoa 2009). However, it has been most strongly emphasized in an influential set of models addressing the ego depletion phenomenon. According to the strength model of self-control introduced by Baumeister and colleagues (e.g., Muraven & Baumeister 2000), depletion—the decline in cognitive performance, engagement, or persistence observed following an earlier bout of vigorous cognitive exertion—reflects a reduction in the availability of a critical resource, a resource required for and consumed by the exertion of control. Other effects, for

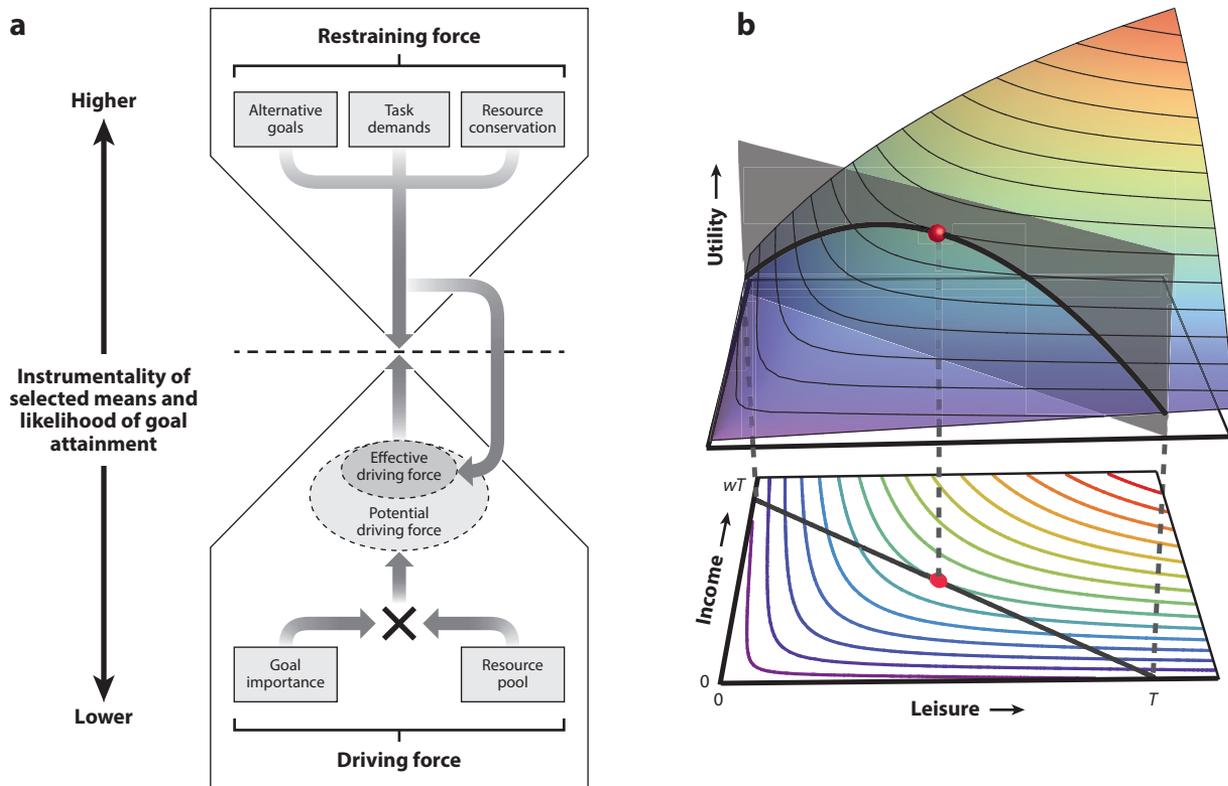


Figure 2

(a) Schematic illustration of the cognitive energetics theory, as proposed by Kruglanski et al. (2012). Invested effort (effective driving force) is jointly determined by a driving force (a function of goal importance and the size of a resource pool) and a restraining force (a function of task demands, other alternative goals, and bias toward resource conservation). (b) The utility surface posited by economic labor supply theory (LST), as discussed by Kool & Botvinick (2014). LST considers decisions about how to allocate time between work and leisure. Work is assumed to yield income via a wage. Leisure is assumed to have its own inherent value, which can also be conceptualized as the value of avoiding the effort costs associated with work. A particular combination of income and leisure time corresponds to a point in a plane, as shown at the bottom of the diagram. Time-allocation decisions are assumed to be constrained by a time budget, indicated in the figure by the diagonal line segment lying within this plane. LST proposes that when the value or utility attaching to all possible combinations of income and leisure are plotted, what results is a concave utility function, as shown in the upper half of the figure, with iso-utility contours projected into the plane below. Time-allocation decisions locate the point of maximum utility along the constraint line. The concavity of the utility function means, in effect, that there is a preference for combinations of income and leisure that balance between these two. LST makes strong predictions concerning the impact of time-allocation decisions on wage changes. Kool & Botvinick (2014) tested a core set of such predictions in a context where “work” corresponded to the exertion of cognitive control and found incentive effects matching those predicted by labor supply theory. (a) Adapted with permission from Kruglanski et al. (2012). (b) Adapted with permission from Kool & Botvinick (2014). Abbreviations: T , maximum time available for leisure; wT , maximum attainable income.

example the reduction in performance sometimes seen in anticipation of later requirements for cognitive effort, are attributed to a strategic conservation of this resource for later use (Muraven et al. 2006).

In some work wielding the resource construct, the resource in question is characterized in abstract functional or computational terms (see, e.g., Persson et al. 2013). However, within the

Labor supply theory:

a formal framework, deriving from microeconomics but recently applied to the study of cognitive control, that addresses the question of how workers choose to divide their time between labor and leisure

strength model, it has been identified with blood glucose. The exertion of control is proposed to reduce glucose levels, depriving of necessary fuel the neural circuits underlying control function (Muraven & Baumeister 2000). Some initial evidence for the role of glucose was provided in studies that found glucose administration reversed the depletion effect (Gailliot et al. 2007). However, as discussed below, subsequent findings have given rise to considerable controversy.

Reward-Based Models

A third perspective on the interface between motivation and cognitive control centers on the theme of reward maximization. This approach views the operation of the control as involving an ongoing series of decisions, each aimed at maximizing expected utility. An important assumption that enters into most reward-based models is that decision making weighs both the anticipated rewards and anticipated costs of specific control operations. The rewards in question are the payoffs associated with good performance in the target task (for example, in an experimental context, bonus payments accrued for correct responses). The costs, in turn, are those inherent to the mobilization of cognitive control. What results is naturally viewed as a cost-benefit analysis, in which the benefits of cognitive control are weighed against its drawbacks.

In the behavioral economics literature, this cost-benefit analysis has sometimes been formalized in terms adopted from labor supply theory. In pioneering work along these lines, Smith & Walker (1993) introduced what has since been referred to as the labor theory of cognition. Here, cognitive effort, viewed as a form of work, is mobilized to a level that maximizes the difference between prospective rewards and inherent effort costs.

Closely related models have emerged from work drawing on optimal control and reinforcement learning theory (see Dayan 2012). For example, in recent work Shenhav et al. (2013) presented a theory centering on the concept of the expected value of control (EVC). Generalizing tools from reinforcement learning, Shenhav and colleagues defined EVC as the cumulative reward expected to follow from directing control in a particular direction with a particular intensity, less the expected cost of this exertion of control. The EVC theory proposes that decisions within the realm of cognitive control are selected so as to optimize the EVC. Like overt motor actions, the cognitive actions underlying control function are understood to arise from a cost-benefit analysis aimed at maximizing expected reward.

As simple and intuitive as the notion of a cost-benefit analysis may be, in the context of cognitive control it can accommodate a surprising amount of nuance. Work by Camerer & Hogarth (1999), for example, has described how the Smith & Walker (1993) labor theory of cognition might be elaborated to take into account individual differences in domain-specific processing capacity or cognitive skills, a potentially important step given that such individual differences plausibly mediate the relationship between cognitive effort and performance (see also Awasthi & Pratt 1990, Palacios-Huerta 2003, Rydval 2011). The cost-benefit framework can also be elaborated to implement the notion that control costs may be history dependent—i.e., they may vary as a function of how much control has been exerted in the recent past—which allows the framework to address behavioral effects historically attributed to essentially nonmotivational constructs such as cognitive fatigue or resource depletion (see Boksem et al. 2006, Inzlicht et al. 2014, Tops et al. 2004).

A particularly rich form of cost-benefit trade-off arises within economic labor supply theory. Here, the benefits of work are weighed against its inherent costs in a nonlinear fashion, such that the more one is already working, the more income one demands for a further increment in work effort (**Figure 2b**). In the context of this nonlinear trade-off, effort allocation can be understood as striking a balance between the payoffs of work and the inherent value of leisure. On an empirical level, this aspect of labor supply theory gives rise to detailed predictions concerning the effect of

incentive manipulations on effort allocation. In recent work, Kool & Botvinick (2014) confirmed that these predictions hold in the case of cognitive effort, just as they have been shown to hold in labor markets.

From Metaphor to Mechanism

The force-field, resource, and reward-based perspectives need not be seen as mutually exclusive alternatives. Indeed, in some instances, it is possible to map directly among the three approaches. For example, CET, a force-field-based model, can be brought into approximate alignment with the reward-based model proposed by Kool & Botvinick (2014) if the balance between driving and restraining forces is viewed as an equilibrium point of a dynamical system (e.g., a system of springs). The utility function posited by Kool & Botvinick (2014) becomes a potential energy surface in the CET context. The reward-based model can also be aligned with the resource-based viewpoint by returning to pioneering work on resource theory by Navon & Gopher (1979), which in fact drew on precisely the same mathematical principles as those involved in labor supply theory.

However, despite these approximate parallels, the force-field, resource, and reward-based approaches are not simply notational variants of one another. Substantive differences exist among the three; differences that, in our view, make the reward-based approach appear most promising.

First, when compared with resource accounts, reward-based models have the advantage of being more parsimonious. To make this point concrete, consider the explanation offered by each of these two approaches for the fact that the depletion effect can be prevented by offering strong performance incentives (Muraven & Slessareva 2003). In order to cope with this finding, resource accounts have imported a motivational factor, according to which depletion makes the subject not less able to mobilize control, but simply less willing to do so (see Hagger et al. 2010). This is, in fact, precisely the explanation that has been offered by reward-based accounts (Inzlicht & Schmeichel 2012; Kool & Botvinick 2014; Kool et al. 2010, 2013; Kurzban et al. 2013; Westbrook et al. 2013). In reward-based accounts, the reluctance stems directly from the utility function, which changes shape based on the recent history of effort expenditure (see Kool & Botvinick 2014). In contrast, resource-based accounts rest upon the additional—and frankly unnecessary—assumption that the dynamics of motivation reflect levels of a limited-capacity resource.

Of course, claims based upon parsimony cannot withstand contrary empirical evidence. Resource theories would regain the upper hand if independent evidence could be produced for the existence of a real depletable resource. As it turns out, claims along these lines have been advanced. Specifically, as mentioned briefly above, Baumeister and colleagues (Gailliot et al. 2007, Masicampo & Baumeister 2008) have proposed that the resource underlying behavioral depletion effects and related phenomena is in fact blood glucose. Although this idea has been widely influential, accumulating evidence has seriously undermined its plausibility (for recent critiques, see Inzlicht et al. 2014, Kurzban et al. 2013). Absent a more compelling candidate, the resource in strength theory and related accounts remains an abstract one, manifesting only through its supposed impact on behavior. In this abstract guise, resources have been decried as theoretical “soup stones,” ingredients that have an intuitive appeal but in fact do no real theoretical work (Hockey 1997, Inzlicht et al. 2014, Kurzban et al. 2013, Navon 1984). These and related considerations have led to a recent trend away from resource-based accounts of the depletion effect and toward motivational or reward-based accounts (see Hagger et al. 2010, Inzlicht & Schmeichel 2012, Kurzban et al. 2013).

Reward-based accounts of the relations between motivation and cognitive control also have some apparent advantages over force-field models. As noted previously, force-field theories such as CET can be interpreted in terms that align them with certain reward-based accounts. However,

this transposition ends up highlighting a fundamental difference between the two approaches. Specifically, reward-based accounts center on an optimization process, in which different control operations are compared in terms of their associated net rewards (see Shenhav et al. 2013). In force-field accounts, as represented by CET, cognitive actions are the result of equilibrium being reached between driving and restraining forces. Physics-savvy readers will protest that the equilibria of a dynamical system can often be described as energy minima and that equilibrium attainment can thus be described as the result of an optimization process. The problem is that when this principle is applied to force-field accounts of motivation, the resulting optimization process does not have a transparent psychological interpretation. In short, it is not clear from a psychological point of view exactly what force-field models are optimizing.

This ambiguity can give rise to troubling explanatory lacunae. A concrete example can be drawn from CET itself. Here, as explained previously, an effective driving force rises to meet a resistive force, up to a limit set by a potential driving force. An important detail of the account is that the subject can adjust the resistive force by selection among strategies with different levels of cognitive demand. However, CET does not explicitly specify the basis for strategy choice. Because the theory is not framed in terms of an optimization process, it is difficult for it to explain why one strategy might be preferred over another without moving outside the scope of the force-field mechanism.

For the reasons just reviewed, reward-based theories of the motivation-control interface appear to have an edge over other approaches. However, it must be noted that reward-based theories carry their own special liability. This attaches to the construct of reward itself. Reward-based theories are founded on the idea that behavioral choices reflect comparisons of reward or value. But how are we to know what value an individual places on any choice option? In many settings, the answer assumed is that one may infer such values from the individual's overt choices. There is an obvious risk of circularity here: Choice is explained based on reward, but reward is inferred from choice. Economics has gone to elaborate lengths to extricate itself from this circularity (see Glimcher et al. 2009), but it remains an ineluctable problem for any psychological theory that would leverage the notion of reward (see Padoa-Schioppa 2011).

A similar though less often noted problem attaches to a second construct that is central to many reward-based theories of motivation and control, namely the construct of effort. Effort is a key ingredient in many (if not all) theories relating motivation to cognitive control (e.g., Bettman et al. 1990, Bonner & Sprinkle 2002, Camerer & Hogarth 1999, Hockey 1997, Libby & Lipe 1992). In general, such theories introduce effort as a variable mediating between incentives and performance. This raises the same problem as the reward construct: Effort is purported to explain the relationship between incentives and performance, but it is also measured or inferred from the observed relationship between these two.

The problem becomes deeper when effort is also assumed to carry an inherent cost, an assumption that plays an important role in many theories, as reviewed above. In this setting, the optimal amount of effort to invest is the one that maximizes net reward, i.e., the "income" generated by successful task performance less the cost of effort. However, note that this means that effort actually plays not one but two mediating roles. First, it determines the quality of performance (and thus, indirectly, the performance-dependent income), and second, it scales the cost associated with task engagement. This dual mediating role exacerbates the measurement problem, since it is difficult to independently estimate (or manipulate) the performance-related and cost-related facets of effort.

Fortunately, there is a way out of these quandaries, and this brings us at last to the role of neuroscience. It has been noted in the field of neuroeconomics that neuroscience may offer a solution to the problem of circularity associated with the construct of reward. This solution opens

up, in particular, if there exist measurable neural correlates of subjective value, as current data in fact do suggest (Levy & Glimcher 2012). As Padoa-Schioppa (2011) has argued, “based on behavior alone, values cannot be measured independently of choice. Consequently, the assertion that choices maximize values is intrinsically circular. The observation that values are actually computed in the brain essentially breaks this circularity. Indeed, once the correspondence between a neural signal and a behavioral measure of value has been established, that neural signal provides an independent measure of value, in principle dissociable from choices. In other words, the assertion that choices maximize values becomes potentially falsifiable and thus truly scientific” (p. 335).

Neuroscience appears capable of playing a similar role when it comes to the effort construct. If neural correlates of effort can be identified, this provides a way out of the potential circularity of effort-based explanation. The importance of finding behavior-independent, physiological measures of cognitive effort has in fact been long appreciated in psychophysiology research, where autonomic effects on cardiac, pupillary, and metabolic function have been used to considerable effect as independent measures of effort (e.g., Fairclough & Houston 2004, Silvestrini & Gendolla 2013, Silvia et al. 2014, Wright et al. 2013). These measures are necessarily indirect, serving only as potential biomarkers or reporter variables indicating the level of effort; they clearly cannot mediate the relationship between incentives and performance. But findings from psychophysiology point the way to more central neuroscientific measures through which contact might be made with genuine mediating mechanisms.

If these assertions are correct, if neuroscience offers a way to ground otherwise circular notions of reward and effort, then the role of neuroscience assumes central importance in the study of motivation and cognitive control. Far from being a “special topic” in which neural correlates are sought for settled psychological mechanisms, neuroscience offers to play a more pivotal role, occupying the critical path toward a causally adequate understanding of the motivation-control interface.

NEUROSCIENTIFIC FINDINGS

Having argued, in a preliminary way, for the potential importance of neuroscience in the study of motivation and cognitive control, we turn now to a selective review of key neuroscientific findings in this arena (Beck et al. 2010; for related reviews, see Coutlee & Huettel 2012, Locke & Braver 2010, Pessoa & Engelmann 2010). We begin with some general considerations relating to the anatomical systems involved in control and motivational function. We then revisit the three core behavioral phenomena described previously, this time looking at data concerning their neural underpinnings.

A Tale of Two Systems

The vast majority of neuroscientific research on the relationship between motivation and control adopts what we have termed the reward-based perspective, viewing control operations as guided by a utility-maximization principle. As a result, such work lies at the confluence of two otherwise freestanding research areas within contemporary neuroscience, one focusing on cognitive control and the other on reward-based decision making. As we explain, each of these research areas has come to focus on its own specific network of neuroanatomical structures, and the general approach in work studying the interface between motivation and control has been to ask how the networks relating to reward processing and cognitive control might interact.

Neuroscientific studies of cognitive control have identified a set of cortical and subcortical structures that appear to work together to implement control function. These include subregions of the lateral prefrontal cortex (PFC; dorsolateral, inferior frontal junction, frontopolar), the

Prefrontal cortex (PFC): the front-most portion of the cerebral cortex that contains a number of subregions believed to play a pivotal role in supporting executive function

Ventral striatum:

a subcortical nucleus (cluster of neurons) and component of the basal ganglia that is believed to play a key role in reward processing and motivation

Dopamine (DA):

a neurotransmitter that is broadcast to large portions of the brain, including cortical and subcortical structures, and is believed to play an important role in reward and motivation, effort-based decision making, and cognitive control function

dorsal anterior cingulate and presupplementary cortices, dorsal premotor cortex, the anterior insula, and the intraparietal cortex (Cole & Schneider 2007, Duncan 2010, Niendam et al. 2012, Power & Petersen 2013). A different set of regions, including the ventromedial frontal and medial parietal cortices, has been widely reported to decline in activity during performance of control-demanding tasks and has thus sometimes been referred to as the default mode or task-negative network (Buckner et al. 2008, Fox et al. 2005).

Studies of reward-based decision making have, in parallel, identified a distinct network of relevant structures including ventromedial and orbitofrontal cortex, ventral striatum (including the nucleus accumbens), and amygdala, as well as the ventral tegmental area, the source of mesolimbic and mesocortical dopamine (DA) projections (Bartra et al. 2013, Clithero & Rangel 2014, Liu et al. 2011). Current research is focused in part on specifying which particular aspects of reward and reward-based decision are represented or processed within and across each of these structures, with important distinctions holding between reward and expected-value signals and between representations of value and prediction-error signals related to reinforcement learning (Niv 2009). Despite such subtleties, the ubiquity of reward-related signals in the relevant areas seems to justify viewing them together as a coherent network that is focused in a broad sense upon reward processing.

As stated previously, a great deal of neuroscientific work that focuses on motivation and control attempts to address the question of how the networks dedicated to reward and control might interface or interact in order to give rise to motivational effects in control. This question is far from settled. Indeed, it is too soon to say even whether it is precisely the right question to ask. Nevertheless, a number of interesting ideas about how the networks interrelate have guided the bulk of research to date (for relevant discussion, see Pessoa & Engelmann 2010).

One possibility is that the networks might interact directly, through monosynaptic connections. Anatomical data are certainly consistent with this possibility. For example, strong direct connectivity exists between ventromedial frontal areas involved in reward processing and lateral PFC areas strongly implicated in control (Barbas & Pandya 1989, Cavada et al. 2000), alongside a pathway connecting the two areas via the caudate nucleus (Alexander et al. 1986). Such direct interactions seem consistent with findings, reviewed below, that clearly indicate the presence of reward-related information in neural responses within dorsolateral PFC as well as findings pointing to incentive-induced increases in correlated activity between regions.

However, a number of studies point to the existence of more complex and structured paths between the two networks. One influential idea is that information from ventral cortical areas belonging to the reward network may flow to dorsal control areas via a spiral-like pathway running through the striatum via anatomically asymmetric projections to and from the ventral tegmental areas (Haber et al. 2000). Given that the ventral tegmental area is a major source of dopaminergic inputs to frontal and subcortical targets, its involvement in this spiral pathway points to a potential role for DA in connecting control with motivation (Aarts et al. 2011).

Other findings suggest that the mesolimbic and mesocortical DA system may also play a more direct role in linking cognitive control with reward. It is well established that DA neurons show phasic responses to reward cues (Schultz 1998), whereas tonic DA release has been linked to sustained motivational behaviors (Howe et al. 2013). Widespread connections originating from ventral tegmental area and substantia nigra reach large portions of the cortical surface and subcortical areas, where DA is able to rapidly influence neuronal activity. In particular, DA is known to have a range of effects on cellular physiology, such as altering neuronal excitability (Henze et al. 2000, Nicola et al. 2000) and enhancing the signal-to-noise ratio (Durstewitz & Seamans 2008, Thurley et al. 2008). Such effects in subcortical and cortical targets, including frontal cortex, could potentially facilitate controlled information processing in a number of ways. For example,

DA may sharpen cortical tuning (Gamo & Arnsten 2011), which could have the effect of heightening perceptual sensitivity and enhancing top-down attentional or control signals.

Beyond the potential role of DA, another widely considered possibility is that the reward and control systems may interface within a particular cortical region, which may serve as a hub or convergence zone in linking motivation and control. For example, a voxel-based lesion-symptom mapping study by Gläscher and colleagues (2012) identified a region within medial PFC associated with performance in both reward and cognitive control tasks; the investigators proposed that this region might play a mediating role in linking reward and control networks.

More widely discussed is the potential mediating role of the dorsal anterior cingulate cortex (ACC). This structure has long been known to play a critical role in monitoring action selection and task performance as well as in triggering compensatory adjustments in cognitive control (Shenhav et al. 2013). At the same time, a wide range of evidence indicates that the ACC is involved in reward-based decision making (see Wallis & Kennerly 2011). On the basis of this combination of findings, a number of investigators have proposed that the ACC might play a central role in bridging between reward and control processing. This idea has been cashed out in computational detail in the recent work of Shenhav and colleagues (2013), who propose that the dorsal ACC computes the expected value of control, as defined previously, using this as a basis for selecting among candidate control functions, which are then implemented in other sectors of the lateral PFC. Related work places the ACC in a similar role but additionally emphasizes hierarchical topographic organization. Specifically, a variety of studies have proposed that the lateral PFC may house a discrete set of hierarchically organized subregions, subserving different levels of control function (Badre 2008). Aligning with this perspective, and drawing on a number of anatomical and functional observations, several investigators have suggested that a corresponding hierarchy resides within the medial PFC, which serves to regulate the lateral hierarchy based on motivational inputs (Holroyd & Yeung 2012, Kounieher et al. 2009, O'Reilly 2010, Taren et al. 2011).

The forgoing list of hypotheses concerning the interaction of reward and control networks provides the backdrop for a range of recent neuroscientific studies that examine the relationship between motivation and control. We turn below to a selective review of such work, organizing the relevant studies under three headings that correspond to those employed in our previous synopsis of behavioral findings.

The Relationship Between Incentives and Performance: Neuroscientific Findings

There is now a rapidly burgeoning literature that addresses the neural mechanisms that underlie the effects of incentives on cognitive control. The earliest studies in this area focused on working memory function in nonhuman primates (Kawagoe et al. 2004, Leon & Shadlen 1999, Watanabe 1996, Watanabe et al. 2002). In a representative experiment, Leon & Shadlen (1999) studied a task in which a visual target location had to be recalled following a delay period. As in numerous previous studies, neurons in dorsolateral PFC that code for specific locations were found to display sustained activity over the delay, consistent with a role in working memory maintenance. More importantly, on trials in which large rewards were offered for accurate recall, this delay-period activity was selectively enhanced. These and related results provided the first neuroscientific evidence that motivational signals can modulate core components of cognitive control.

An additional insight from primate neurophysiology studies is that incentive effects on control structures are linked not only to trial-to-trial variations in reward, but also to more temporally extended motivational contexts. For example, work by Watanabe and colleagues (Watanabe 1996, Watanabe et al. 2002) showed that PFC neurons involved in working memory display tonically

Anterior cingulate cortex (ACC): a portion of the cerebral cortex situated on the inner surface of the frontal lobe, which has been implicated in decision making, performance monitoring, and the regulation of cognitive control

elevated baseline activity during trial blocks involving relatively large or preferred rewards, persisting even through isolated trials in which task cues indicate that no reward is available. This suggests that motivational context can exert a sustained influence on PFC activity and that incentives can affect cognitive control in both a trial-by-trial and a contextual (block-based) manner.

The first human neuroimaging experiments investigating incentive effects on control directly followed from the animal work and also focused on working memory (Gilbert & Fiez 2004, Krawczyk et al. 2007, Pochon et al. 2002, Taylor et al. 2004). The general approach in such studies involved independently varying working memory load and trial reward value. Consistent with animal results, this approach revealed that high-reward conditions selectively amplify delay-period activity within the lateral PFC, parietal cortex, and other components of the brain cognitive control network.

Further work has shown that these effects extend to cases in which the role of working memory is to maintain a representation of the currently relevant task. For example, Dixon & Christoff (2012) used functional magnetic resonance imaging (fMRI) adaptation methods to show that activity in lateral PFC is sensitive to the conjunction of task rule and trial reward value, such that activity was modulated only when there was repetition of both dimensions. Etzel and colleagues (J.A. Etzel, M.W. Cole, J.M. Zacks, K.N. Kay & T.S. Braver, manuscript submitted) used fMRI pattern classification methods to demonstrate that task rules could be decoded more effectively on incentive trials compared to intermixed nonincentive trials. Moreover, the patterns of activity associated with each task were more distinct from each other, which suggests that incentives induced a sharpening of task representations. This sharpening effect was further observed to statistically mediate reward-related enhancements in behavioral performance.

Although the typical experimental approach in these studies is to manipulate incentives on either a block-wide (e.g., Pochon et al. 2002) or trial-by-trial basis (e.g., Taylor et al. 2004), some studies have orthogonally combined these two tactics in order to directly isolate the effects of motivational context (e.g., Kouneiher et al. 2009). Echoing the nonhuman primate literature, a number of findings have demonstrated that the motivational context can produce sustained (i.e., persisting across intertrial periods) as well as trial-specific changes in brain activity (Engelmann et al. 2009, Locke & Braver 2008). Using this strategy, Jimura et al. (2010) found selective behavioral performance enhancements and individual differences effects of motivational context, which were statistically mediated by a shift in lateral PFC activity dynamics from a transient mode (activated late in the trial, during the response period) to a sustained and anticipatory mode (activated both tonically and early in the trial during working memory updating).

In addition to studies of working memory, incentive manipulations have now been the focus of human cognitive neuroscience investigations across a wide variety of cognitive control domains, including strategic encoding in episodic memory (Adcock et al. 2006, Wittmann et al. 2005), selective attention (Engelmann et al. 2009, Krebs et al. 2012, Mohanty et al. 2008, Small et al. 2005), response inhibition (Boehler et al. 2014, Padmala & Pessoa 2010), context processing (Kouneiher et al. 2009, Locke & Braver 2008), conflict processing (Krebs et al. 2013, Padmala & Pessoa 2011, Stürmer et al. 2011), and task switching (Aarts et al. 2010). In addition, although the approach has generally been used to study the impact of positive or appetitive incentives, it has also been extended to settings involving negative incentives or threats (Dreisbach & Fischer 2012; Engelmann et al. 2009; Guitart-Masip et al. 2012a,b; Krawczyk & D'Esposito 2013; Murty et al. 2012; Simoes-Franklin et al. 2010; Taylor et al. 2006). Together with the pioneering results from nonhuman primate research, the results of such studies largely support the view that motivational signals enhance cognitive control functions by sharpening how task goals and other task-relevant information are represented, maintained, and utilized within lateral PFC and associated regions of the brain's control network.

Convergent evidence suggests that these effects within the control network are driven by input from the set of brain areas we have referred to collectively as the reward network. A particularly clear demonstration is provided by the study by Padmala & Pessoa (2011) introduced previously (see also Kinnison et al. 2012, Pessoa 2009, Pessoa & Engelmann 2010). Here, incentive cues occurring before the imperative stimulus were found to trigger activity in core components of the reward network (dopaminergic midbrain, caudate/putamen, and nucleus accumbens) as well as in lateral frontoparietal components of the control network. More strikingly, during the same period these two sets of regions also showed increased functional connectivity, with a particularly strong effect occurring between the right nucleus accumbens and the right inferior parietal sulcus, a region associated with goal-directed visual attentional selection. On the basis of this and related findings, Padmala & Pessoa (2011) proposed a model in which reward cues trigger motivational signals in subcortical reward structures, which then provide a source of increased drive to frontoparietal cognitive control regions, enabling more effective utilization of control processes.

Consistent with theories introduced previously, evidence suggests that the ACC may serve as a key interface between reward and control networks (Kouneiher et al. 2009, Vassena et al. 2014). For example, Rowe et al. (2008) examined the effect of reward expectancy in a task where participants monitored targets in both visual and spatial dimensions. When task events signaled an increasing opportunity for reward on one dimension, rising ACC activity was observed along with a greater behavioral bias toward the relevant target dimension. Moreover, the increase in ACC activity was accompanied by a shift in connectivity between the dorsolateral PFC and other PFC regions associated with each dimension (left ventrolateral PFC for verbal, bilateral superior PFC for spatial). These results were interpreted as indicating that the ACC provides a source of excitatory drive that results in increased connectivity selectively between task-relevant processing regions.

Alongside the ACC, midbrain DA has also been postulated as a source of motivationally triggered control modulation. As Braver and colleagues have observed (Braver 2012, Braver et al. 2007), the most common finding in studies of incentive manipulations is that neural activity is modulated in a preparatory manner—i.e., prior to when responses are required—either through amplified cue and delay-related responses (to contextual, task, or working memory information; Gilbert & Fiez 2004, Padmala & Pessoa 2011) or through sustained activation (Engelmann et al. 2009, Locke & Braver 2008). In some studies, such as that of Jimura et al. (2010), a shift in activity dynamics is observed (see also Beck et al. 2010, Chiew & Braver 2013). Together, these findings suggest that reward incentives primarily target proactive (i.e., preparatory) control processes. Building on this point, Braver and colleagues (Braver 2012, Braver et al. 2007) proposed a theory of dual mechanisms of control, under which proactive control processes reflect context-triggered updating and active maintenance of task goals in lateral PFC and are dependent upon phasic and tonic DA modulation of PFC neuronal activity. As a consequence, the account postulates that motivation signals, reflected in terms of phasic and tonic DA release, should lead to a preferential enhancement of proactive control. Consistent with this view, human studies of motivation and control interactions have consistently observed incentive-linked activity in DA nuclei that predicts performance in control-demanding tasks (Aarts et al. 2010, Adcock et al. 2006, Krebs et al. 2012).

A somewhat different role for DA arises from theoretical work implicating tonic DA release in the vigor (i.e., intensity, speed) of responding (Niv et al. 2007). Under this account, tonic DA encodes the long-run average reward rate of the environment. High reward rates create an opportunity cost for sloth, such that all actions (even those that are unrewarded) are performed with higher vigor (i.e., faster latencies) in order to attain more rewards per unit time. Experimental support for this account has been provided in studies showing that during an oddball target-discrimination task, the long-run average reward value (across minute timescales) had a distinct

influence on task reaction times (Guitart-Masip et al. 2011) and that this effect is modulated by pharmacological manipulation of DA levels (Beierholm et al. 2013).

In addition to its potential enhancing role, DA has also been suggested to mediate in reward-induced decrements in performance, as seen in the phenomenon of choking under pressure. For example, Mobbs et al. (2009) examined the effect of large versus small incentives during performance of a control-demanding task. Compared to low-incentive trials, high-incentive trials were associated with both poorer performance and increased activity in the DA midbrain and dorsal striatum. Moreover, these effects were linked, in that participants showing the strongest responses in these regions also showed the largest incentive-linked performance decrements. These results were interpreted as indicating an overmotivation effect, with an imbalance between activation in subcortical (reward-related) versus prefrontal (cognitive) regions leading toward a shift from more goal-directed to habitual guidance of behavior (see also Aarts et al. 2014; for an alternative account, see Chib et al. 2012).

Control Dynamics: Neuroscientific Findings

At the behavioral level, motivation impacts the dynamics of cognitive control on both short timescales, through performance monitoring, and longer timescales, as in the ego-depletion effect. In both cases, the impact of motivation on control dynamics is readily evident in studies of the underlying neural mechanisms.

A direct neural manifestation of trial-by-trial performance monitoring is the so-called error-related negativity (ERN), a deflection in the electroencephalogram (EEG) arising in conjunction with error commission in speeded-response tasks. Effects of incentives on ERN magnitude have been observed in several studies. Hajcak et al. (2005), for example, observed a larger ERN on trials where a large reward for correct performance was at stake relative to trials involving a smaller potential reward (see also Stürmer et al. 2011). In a second experiment in the same report, a similar effect on ERN magnitude was observed when participants were told that their performance would be monitored and later compared with that of other participants. Bengtsson et al. (2009) observed a related effect by using fMRI. Here, participants who were informed that their cognitive ability was being assessed showed increased error-associated activity in dorsal ACC and lateral PFC relative to subjects performing the same task without the assessment cover story (see also Legault & Inzlicht 2013).

In addition to driving trial-to-trial shifts in control, performance monitoring can display its own longer-term dynamics. In particular, error monitoring can lapse with increasing time on task. This pattern was shown, for example, by Boksem et al. (2006), who observed a steady reduction in posterror slowing over the course of two hours performing a cue-validity task. Through concurrent EEG recording, the same study revealed a concurrent reduction in the magnitude of the ERN. A parallel reduction was seen in the N2, which is widely interpreted as an ERP correlate of conflict detection. Consistent with a motivational interpretation of these effects, the magnitude of posterror slowing returned to baseline when monetary performance incentives were introduced. Among subjects who responded to these incentives primarily by increasing accuracy, a restoration of ERN amplitude was also observed.

Although Boksem and colleagues (2006) characterized these findings in terms of mental fatigue, similar temporal dynamics are involved in what has been referred to as ego depletion, as introduced previously. Here again, a weakening of error monitoring is observed at the neural level. For example, Inzlicht & Gutsell (2007) found a reduction in ERN amplitude in a Stroop task when this task was performed following a depleting emotion-suppression task.

Depletion effects, however, are postulated to involve more than a reduction in performance monitoring following sustained cognitive exertion: They are understood to involve a wholesale reduction in the vigor of cognitive control. A number of studies have endeavored to identify neural substrates of the depletion effect. Although the findings of such studies have been somewhat inconsistent, they nonetheless provide some interesting leads. One neural effect that might be expected to accompany behavioral depletion is a reduction in activation within portions of the executive network. Persson et al. (2013) reported findings along these lines in an fMRI study. Participants performed a verb-generation task both before and after a task that depleted working memory. Compared with a control group that performed a less demanding intervening task, the depleted group showed a reduction in task-induced activity in left inferior PFC, ACC, caudate nucleus, and cerebellum following the working memory task, alongside an increase in reaction times on trials associated with high control demands. Interestingly, this study also observed increased activity in the homologous right inferior PFC region, which suggests that under some circumstances depletion may induce not a simple reduction in frontal function but instead a redistribution of activity.

Another fMRI study, by Wagner et al. (2013), suggests that depletion can involve changes in the functional connectivity between prefrontal control areas and other cortical areas with which they communicate. Here, after performing a cognitively depleting attention control task, a group of dieters showed enhanced orbitofrontal cortex responses to images of food items, but this effect was accompanied by reduced functional connectivity between orbitofrontal cortex and both right and left inferior frontal cortex. The authors interpret this finding as reflecting a reduction in top-down control of reward representations in orbitofrontal cortex.

As mentioned previously, a wide range of studies have reported an inverse relationship between activity in the executive network and a different set of regions, including ventromedial PFC and posterior cingulate cortex. Because the latter network tends to become more active when the subject is at rest, i.e., not engaged in effortful, controlled information processing, it is often referred to as the default mode network (Buckner et al. 2008). Given the initial evidence that depletion involves reductions in executive network engagement (or connectivity), it seems reasonable to anticipate that it should also be associated with an increase in activity within the default mode network. Such an effect has indeed been recently observed in an fMRI study by Esposito and colleagues (2014), who found that inducing mental exhaustion—resulting from sustained performance of a novel task—led to both increased activity (resting-state fluctuations) in the default mode network and decreased activation of the frontoparietal executive network.

The Cost of Control: Neuroscientific Findings

The exertion of cognitive control is experienced as subjectively costly, as demonstrated in terms of demand-selection and economic discounting phenomena described above. A number of neuroscientific studies have begun to uncover the neural basis of how such control costs are registered and of the decision-making mechanisms that are sensitive to these costs.

The relevant work arises alongside a more mature literature on the cost of physical exertion. The idea that physical effort is associated with subjective disutility has a very long history and a rich bed of empirical support. Neuroscientific studies have yielded a number of clues concerning the underlying neural mechanisms. First, the ACC seems to be an important hub for physical effort-based decision making, as indicated by a decreased willingness to engage in physical work to earn rewards following ACC lesions (Walton et al. 2006) as well as by the finding that some ACC neurons code for physical effort demands during effort-based decision making (Hosokawa et al. 2013). A second key set of observations relates to the role of the midbrain DA system. In

the ventral striatum and ACC, DA levels appear to modulate effort-based decision making, as indicated by a shift toward reduced willingness to engage in physical effort for reward when DA inputs to these structures are blocked (Salamone et al. 2012).

Initial studies have suggested that the circuitry underlying cognitive effort-based decision making overlaps with that relating to physical effort, but it is also partially distinctive (see Schmidt et al. 2012). Botvinick et al. (2009) performed one of the first studies focusing on neural signals reflecting the cost of cognitive control. Participants performed cognitive tasks to earn monetary rewards, and ventral striatum activity was found to increase at the time of reward delivery. Critically, however, the response strength was modulated by the degree of cognitive effort required to attain the reward. Specifically, reward responses were reduced when a high degree of mental effort had been required by the task, an apparent neural correlate of cognitive effort discounting, in which the subjective value of a reward is decremented by the cost in effort required to attain it (for a later replication of this effect in the context of physical effort, see Kurniawan et al. 2013). Consistent with this interpretation, Botvinick and colleagues (2009) and Kool et al. (2013) observed that ventral striatal reward responses correlated negatively with the degree of activity in both ACC and dorsolateral PFC during performance of the foregoing cognitive task.

Further research has revealed a role for both ACC and dorsolateral PFC in driving cognitive demand avoidance in decision making. In one study, Magno and colleagues (2006) presented participants with a series of attention-demanding search arrays and, for each array, gave participants the choice to identify the presence or absence of a target or to indicate that they would prefer to forgo the search on that trial. fMRI revealed elevated activity in both dorsal cingulate and dorsolateral PFC on trials in which the participant actively chose to forgo rather than engage for potential reward. Similarly, McGuire & Botvinick (2010; see also Kool et al. 2013) found that the degree to which performance of a cognitively demanding task engaged these regions predicted the extent to which that same task would later be avoided. Together, these findings are consistent with a role for both dorsal ACC and dorsolateral PFC in cost-sensitive decision making related to the exertion of cognitive control (for related findings implicating anterior insular cortex in effort monitoring, see Otto et al. 2014).

As mentioned previously, Shenhav et al. (2013), focusing specifically on the dorsal ACC, proposed that a core function of this structure is to compute the expected value of control, which is the difference between (*a*) the rewards expected from mobilizing control with a particular direction and intensity and (*b*) the inherent cost associated with this mobilization. Here again, a direct analogy holds with data relating to physical effort costs. For example, Hosokawa et al. (2013) reported neurons in macaque ACC that coded the value of chosen actions, net the cost of physical effort. In a human fMRI study, Croxson and colleagues (2009) observed an analogous integration between reward and effort demands in dorsal ACC, alongside signals correlating with net value in both ventral striatum and midbrain.

One open question concerns the neural events that underlie the ultimate decision to engage in (or avoid) an activity based on its associated cognitive costs. Some initial insight on this question comes from an fMRI study by Schouppé et al. (2014). Here, participants chose repeatedly between performing more and less demanding cognitive-perceptual (flanker) tasks. At moments when participants chose the higher-demand option, greater activity was observed in the striatum, including nucleus accumbens, than when the lower-demand option was chosen. Further research is needed to clarify the import of this finding, partially because choosing high demand options involves overriding a prepotent choice bias (a factor that might in itself explain the fMRI finding) and partially because the finding contrasts with results from a seemingly parallel study focusing on physical rather than cognitive effort (Kurniawan et al. 2010). Nevertheless, the striatum would

appear to be a plausible candidate to mediate in effort-based choice, given the key role it is widely believed to play in go/no-go decisions in general (Frank & Claus 2006).

DISCUSSION

As the foregoing review has no doubt made clear, neuroscientific research into the relationship between motivation and cognitive control is still in its early stages. However, in addition to the many interesting leads provided by existing studies, a few broad conclusions can be drawn.

First, taken together, existing neuroscientific results appear most consistent with a reward-based perspective on control function. Though perhaps not entirely incompatible with alternative force-field or resource-based accounts, the available results from neuroscience resonate strongly with the view that cognitive control represents a domain of reward-based decision making within which operations are selected based on decision mechanisms related to those involved in other forms of reward-based choice. At an implementation level, the available data strongly suggest that motivational effects in control reflect interactions between two large-scale brain networks, one centrally involved in representing reward value and the other involved in implementing control function. Although many details remain to be established, several neural structures, including dopaminergic projections, ventral striatum, ventromedial PFC, lateral PFC, and ACC appear to serve as critical channels for control-relevant motivational signals.

Given that the data so far accumulated indicate that cognitive control may share some mechanisms in common with reward-based decision making in other domains, an inviting direction for future work will be to investigate whether recent discoveries relating to reward-based choice at large might also have relevance for other aspects of control function. For example, an important recent development in the study of reward-based decision making has involved drawing a clear, computationally explicit distinction between a model-free decision, in which actions are selected on the basis of stored value representations, and a model-based decision, in which a knowledge of action-outcome relationships is used to anticipate long-run consequences of candidate actions (Daw et al. 2005). Neural correlates have begun to be uncovered for these two forms of reward-based decision (Dolan & Dayan 2013). An interesting question for future work is what relevance the model-free versus model-based distinction might have to the interface between motivation and cognitive control (see Shenhav et al. 2013). Model-free operation of control raises the amusing possibility that control function may, in some sense, be habitual (a description that fits some recent models of control function; e.g., Frank & Badre 2012). Thinking of control in model-based terms, on the other hand, points to potential new links between metacognition and reinforcement learning.

A second general conclusion from the available neuroscientific data, again consistent with reward-based behavioral models, is that the exertion of control carries an intrinsic subjective cost and that this cost plays an important role in shaping control function. This helps explain what might otherwise be a mysterious aspect of control function: the fact that people do not always invest the maximum amount of effort in cognitive tasks they have chosen to perform. More generally, it suggests a view of control function that centers on an ongoing cost-benefit analysis, in which the potential rewards of control engagement are weighed against its inherent disutility. This, in turn, provides a framework for characterizing the impact of incentives on control function as well as the role of performance monitoring in triggering shifts in control (Shenhav et al. 2013). In particular, rising incentives can be understood as making it “worth it” to increase the strength of control and to accept the greater subjective cost that such a control inherently involves; performance monitoring can be viewed as tracking the relationship between the amount of control invested and the resulting payoff at the level of incentivized performance.

A third conclusion relates to the longer timescale dynamics of control, and in particular to the so-called depletion effect. As we have discussed, behavioral research has recently begun to move away from the idea that depletion reflects diminished levels of glucose or some other metabolic resource and has turned instead to the idea that it may arise from motivational factors. Neuroscientific data, although currently sparse, encourage this reorientation by showing that depletion is not generally accompanied by overall reductions in brain activity (as a metabolic account would predict) and that it involves changes in activity both in reward networks and in centers that have been linked with control costs.

Neuroscience data not only are being used to corroborate and elaborate ideas flowing from behavioral research, but they also hold out the possibility—admittedly, not yet fully realized—of grounding abstract constructs such as reward and effort in concrete and experimentally accessible mechanisms. In this sense, neuroscience holds the potential to play a similar role in the study of motivation and control that it has been argued to play in economics, where progress has been made toward grounding the notoriously elusive construct of subjective utility (Padoa-Schioppa 2011). Indeed, in the case of reward, the relevant findings are essentially the same as those pertinent to economics, because the reward circuits underlying motivational effects in control appear to strongly overlap with those involved in other varieties of reward-based choice (e.g., frontostriatal pathways involving DA midbrain, nucleus accumbens, ventromedial PFC, lateral PFC, and dorsal ACC). A particularly exciting opportunity relevant to grounding the reward construct is presented by the emergence of new techniques available in nonhuman animal research for selectively activating and inhibiting neurons purported to carry reward signals. Optogenetics, for example, has already allowed a clear demonstration of the causal role of dopaminergic neurons in driving motivated behavior in rodent models (Ilango et al. 2014). Applying comparable causal methods to reward circuits in the context of cognitive control research might prove extremely useful in establishing the relevant neural mechanisms.

We have argued that, as in the case of reward, neuroscientific data might also be useful in grounding the evasive construct of effort. It seems clear, from the available evidence, that cognitive effort is closely tied to engagement of the executive control network, spanning dorsolateral PFC, ACC, and intraparietal cortex. However, a great deal more information will be needed before the notion of effort can be fully cashed out into neural events and mechanisms. One challenge, for example, will be to disentangle the neural correlates of effort in its role as a mediator between task demands and performance and in its role as a carrier of intrinsic disutility. Another will be to determine how the neural mechanisms underlying these functional aspects of effort relate to those giving rise to the subjective experience of effort (Kurzban et al. 2013). On these and other fronts, the project of translating effort into neural terms may benefit from the application of causal neural techniques available for human research, such as transcranial magnetic stimulation and transcranial direct current stimulation, approaches that are becoming more widely utilized in studies of cognitive control and motivation (Reinhart & Woodman 2014, Sarkis et al. 2014).

Throughout the present review, we have argued that neuroscience opens up a new horizon in the study of motivation and control. However, it is important to note that the converse holds as well: Ideas and findings from behavioral research present a range of open opportunities for neuroscientific investigation. For example, the social-personality literature has provided a wealth of data concerning the central role of goal representations as mediating between motivation and behavior (Fishbach & Ferguson 2007, Hockey 1997, Locke & Latham 2013). The goal construct has, to date, been considered in a relatively simplified manner within neuroscience (i.e., in terms of simple task rules). However, available methods present the opportunity to investigate the activation and representation of task goals, testing whether goal-related mechanisms, potentially reflected in lateral PFC activation dynamics, might serve as the primary causal nexus of motivational influences

on cognitive control. One important construct in behavioral research on goals, which to our knowledge has been neglected in neuroscientific work, is that of goal commitment, the discrete shift from goal selection to goal pursuit (Nenkov & Gollwitzer 2012). Also important in the behavioral literature on goal setting has been the apparent potency of implicit or nonconscious goal priming (Custers & Aarts 2010, Silvestrini & Gendolla 2013), including the impact of subliminally presented reward cues, which have been clearly shown to impact control function (Zedelius et al. 2014). Understanding the neural substrates of such behavioral factors will form an important part of the project of understanding how motivation impacts cognitive control.

Another behavioral finding that presents an interesting opportunity for neuroscientific research is that the impact of incentives on controlled information processing can depend strongly on how those incentives are framed. This idea has been most fully elaborated within regulatory fit theory (Higgins 2000), which suggests that a promotion focus (a focus on advancement and accomplishment) should produce better performance when incentives are framed in terms of monetary gain than when they are framed in terms of the avoidance of loss, whereas a prevention focus (a focus on safety and security) should produce the converse pattern. Maddox & Markman (2010) further observed that nonlinear effects on cognitive control can result when incentives differ at local and global levels, for example when one is offered a monetary reward (an appetitive incentive) if one can sufficiently avoid errors in a cognitive task (an avoidance goal). Understanding how such structured motivational contexts impact control function at the neural level constitutes an interesting target for future research.

All in all, the recent surge of interest in the relationship between motivation and control has led to enlightening results in both behavioral and neuroscientific research. In coming years, the challenge will be to build increasingly robust bridges between neuroscience and psychology, refining our understanding of how incentives shape control function and of the causal mechanisms that underlie the relevant effects.

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