An integrative effort: Bridging motivational intensity theory and recent neurocomputational and neuronal models of effort and control allocation

Silvestrini, N.; Musslick, S.; Berry, A.S.; Vassena, E.

2023, Article / Letter to editor (Psychological Review, 130, 4, (2023), pp. 1081-1103)

Doi link to publisher: https://doi.org/10.1037/rev0000372

Psychological Review

ISSN: 0033-295X

2023, Vol. 130, No. 4, 1081–1103
https://doi.org/10.1037/rev0000372

THEORETICAL NOTE

An Integrative Effort: Bridging Motivational Intensity Theory and Recent Neurocomputational and Neuronal Models of Effort and Control Allocation

Nicolas Silvestrini[1], Sebastian Musslick[2, 3], Anne S. Berry[4], and Eliana Vassena[5, 6]
[1] Geneva Motivation Lab, Faculty of Psychology and Educational Sciences, University of Geneva
[2] Department of Cognitive, Linguistic, and Psychological Sciences, Brown University
[3] Carney Institute for Brain Science, Brown University
[4] Department of Psychology, Brandeis University
[5] Experimental Psychopathology and Treatment, Behavioural Science Institute, Radboud University
[6] Donders Institute for Brain, Cognition and Behaviour, Radboud University

An increasing number of cognitive, neurobiological, and computational models have been proposed in the last decade, seeking to explain how humans allocate physical or cognitive effort. Most models share conceptual similarities with motivational intensity theory (MIT), an influential classic psychological theory of motivation. Yet, little effort has been made to integrate such models, which remain confined within the explanatory level for which they were developed, that is, psychological, computational, neurobiological, and neuronal. In this critical review, we derive novel analyses of three recent computational and neuronal models of effort allocation—the expected value of control theory, the reinforcement meta-learner (RML) model, and the neuronal model of attentional effort—and establish a formal relationship between these models and MIT. Our analyses reveal striking similarities between predictions made by these models, with a shared key tenet: a nonmonotonic relationship between perceived task difficulty and effort, following a sawtooth or inverted U shape. In addition, the models converge on the proposition that the dorsal anterior cingulate cortex may be responsible for determining the allocation of effort and cognitive control. We conclude by discussing the distinct contributions and strengths of each theory toward understanding neurocomputational processes of effort allocation. Finally, we highlight the necessity for a unified understanding of effort allocation, by drawing novel connections between different theorizing of adaptive effort allocation as described by the presented models.

Keywords: effort, cognitive control, expected value of control, meta-learning, reinforcement learning

Supplemental materials: https://doi.org/10.1037/rev0000372.supp

Almost every day we encounter challenging situations where we have to strive for our goals. Performing difficult cognitive or physical tasks, remaining calm in front of our excited kids, or staying committed to a healthy lifestyle are examples of behaviors that require cognitive and/or physical effort to be successful and that may consequently increase cardiovascular reactivity associated with effort. In this article, we aim to integrate recent neurocomputational theories of effort allocation with a long-standing theoretical framework of resource mobilization, namely motivational intensity theory (MIT; Brehm, 1975; Brehm et al., 1983; Brehm & Self, 1989). From different angles, these theories seek to explain the mechanisms underlying the motivation to engage in effortful behavior. Despite the intuitive overlap in scope, no attempt at integration has been made so far. A unifying account of effort allocation may have critical implications for the short-term or long-term consequences of effort and could help understand phenomena such as mental fatigue (Wright, 2009; Wright & Mlynski, 2019) and performance decrements over time (Boksem et al., 2005). Further, it could provide insights into the neurocognitive mechanisms linked to the onset of cardiovascular diseases

---

Nicolas Silvestrini https://orcid.org/0000-0002-5654-9428
Sebastian Musslick https://orcid.org/0000-0002-8896-639X
Eliana Vassena https://orcid.org/0000-0002-5761-6813

Sebastian Musslick, Anne S. Berry, and Eliana Vassena shared last authorship.

The authors have no conflict of interest to disclose. Previous ideas appearing in this article were discussed at a symposium entitled, “Neural mechanisms of effort mobilization and cognitive control” at the International Convention of Psychological Science, Paris, France, 2019, involving the four authors of this article. A preprint of this article was uploaded on PsyArXiv on September 2021 (https://psyarxiv.com/gn37y/). Eliana Vassena would like to thank Massimo Silvetti for his input and help with the RML simulations and framework. The code for computational implementation of EVC theory for framing predictions in terms of MIT is available at https://github.com/musslick/MIT_EVC. The code for RML simulations presented in this manuscript is available upon request. This manuscript does not report any original study and did not involve any preregistration.

Correspondence concerning this article should be addressed to Nicolas Silvestrini, Geneva Motivation Lab, Faculty of Psychology and Educational Sciences, University of Geneva, bd. du Pont d’Arve 40, Geneva CH-1205, Switzerland. Email: nicolas.silvestrini@unige.ch

(see Gendolla & Richter, 2004; Kop, 1999) and stress-related neuropsychiatric disorders (where motivational deficits manifest as prominent and invalidating symptoms, e.g., Husain & Roiser, 2018; Treadway et al., 2012).

As described in detail later on, the core idea of MIT is that individuals avoid wasting resources and therefore calibrate their effort considering the difficulty and the importance of the task at hand. In this article, we will summarize evidence supporting these predictions mainly based on cardiovascular measures of effort (e.g., Gendolla, Wright, et al., 2012; Richter et al., 2016; Wright, 1996). More recent models aim to explain similar processes from a different conceptual and methodological perspective. Whereas MIT is concerned with the broad motivational determinants of effort, recent models focus on the interaction between motivation and cognitive control (Botvinick & Braver, 2015; Manohar et al., 2015; Shenhav et al., 2013, 2017; Verguts et al., 2015) and explore neurocognitive processes associated with resource mobilization (e.g., Sarter et al., 2006; Shenhav et al., 2013; Silvetti et al., 2018). Building on a large body of behavioral, computational, and neuroimaging studies, these models propose mechanisms for how individuals determine the intensity of cognitive control or effort (Sarter et al., 2006; Shenhav et al., 2013; Silvetti et al., 2018) that is worth allocating and describe the brain networks involved in computing the relevant information to adjust behavior.

Our aim is to integrate insights from MIT with the underlying cognitive, computational, and neural processes proposed by recent models of cognitive control and effort. This review serves to critically compare MIT with such models and demonstrates that MIT remains a useful tool for predicting effortful behavior. Integrating recent neurocognitive models with MIT has the potential to inform cognitive and neural processes that determine effortful behavior including effort-related cardiovascular adjustments. In addition, deriving a formal relationship between these theories may help establish connections between different levels of analysis (ranging from cognitive to neurobiological and neuronal) to better characterize adaptive effort allocation.

Drawing on the cognitive control and neuroscience literature, recent work suggested that effort and effort-related cardiovascular reactivity are mainly driven by the dorsal anterior cingulate cortex (dACC), which is predicted to combine information about costs and benefits to determine and drive optimal behavior adjustments (Silvestrini, 2017). This hypothesis about dACC function was mainly drawn from the conflict monitoring theory (Botvinick et al., 2001, 2004) and the expected value of control (EVC) theory (Shenhav et al., 2013, 2016). In this article, we aim to go a step further by discussing the specific predictions of these theories in relation to MIT predictions. Moreover, we discuss a plausible neurobiological implementation of these mechanisms, proposed by the reinforcement meta-learner (RML) theory of dACC function (RML; Silvetti et al., 2018), and an alternative neuronal model, the neuronal model of attentional effort (NMAE; Sarter et al., 2006). Whereas providing a detailed comparison of all models would go beyond the scope of this article, we rather aim to integrate the relevant aspects of these models with the long-standing framework of MIT.

In the next section, we introduce definitions and conceptual issues associated with effort and cognitive control. After presenting MIT along with its core assumptions and predictions, cardiovascular operationalizations, and supporting empirical evidence, we describe recent models of effort allocation: the EVC theory (Shenhav et al., 2013), the RML theory (Silvetti et al., 2018), and the NMAE (Sarter et al., 2006). For each model, we discuss how predictions and associated findings converge or diverge with MIT. Finally, we integrate these propositions and findings in a general discussion, drawing attention to the strength and specificity of each theory, notable conceptual differences between recent theories, and open questions and future perspectives.[1]

Effort and Cognitive Control: Definitions

The MIT is concerned with motivational intensity, which determines how much people strive to attain a goal (Geen, 1995). Brehm defined motivational intensity as the momentary magnitude of motivational arousal (Brehm & Self, 1989). Moreover, he presented motivational arousal as the mobilization of energy, energization, or effort. Later on, researchers testing the predictions of MIT focused on the concept of effort (e.g., Gendolla, Wright, et al., 2012; Wright, 1996), defined as the mobilization of resources to carry out instrumental behavior (Gendolla & Wright, 2009). This definition applies to both physical and cognitive effort and refers to resources that can be biochemical (e.g., adenosine triphosphate), psychological (e.g., attention), or physical (e.g., time) in nature (see Silvestrini & Gendolla, 2019). It is assumed that, to achieve their goals, people exert effort by engaging resources and MIT predicts how much resources people mobilize at a particular moment in time.

Early theories of cognitive control propose a distinction between automatic and controlled processes, with the former being experienced as effortless and the latter being experienced as effortful (Norman & Shallice, 1986; Posner & Snyder, 1975; Shiffrin & Schneider, 1977). Automatic processes refer to direct responses to the environment driven by bottom-up processes and stimulus-response associations (Miller & Wallis, 2009). In contrast, cognitive control can be defined as the collection of mechanisms that bias information processing in accordance with current task goals, often in the face of distraction or overriding prepotent responses (Cohen et al., 1990). This and other definitions (Shackman et al., 2011) suggest that cognitive control—an instance of mental effort—involves executive functions such as response inhibition, task switching, and information updating (Jurado & Rosselli, 2007; Miller & Cohen, 2001; Miyake et al., 2000; Niendam et al., 2012). Later theories emphasized that the distinction between controlled and automatic processing is a relative one: a cognitive process is considered more automatic, that is, less effortful, if it interferes less with other cognitive processes (Botvinick et al., 2001; Cohen et al., 1990).

Mounting empirical evidence suggests that the exertion of cognitive control is associated with an intrinsic cost (Botvinick & Braver, 2015; Kool et al., 2010, 2017; Manohar et al., 2015; Westbrook & Braver, 2015). In line with MIT, the models presented in this review all seek to explain how people allocate effort, by describing the decision-making processes underlying the allocation of cognitive control (Shenhav et al., 2013) and by linking these to neural systems that compute such trade-offs (Silvetti et al., 2018) and implement control-demanding behavior (Sarter et al., 2006; Silvetti et al., 2018).

Shenhav et al. (2017) also define cognitive effort as the set of intervening processes that determine which level of performance will

---

[1] This article does not report any original study and did not involve any preregistration.

be attained given the specifics of the task and individual information processing capacity. The framework of MIT highlights what is hinted at in this definition: effort is clearly to be distinguished from performance (e.g., Wright, 1996). First, effort may lead to better performance under certain conditions but is not the only determinant of performance. Other determinants include an individual's capacity or strategy (see Locke & Latham, 1990, 2019). Second, effort may reflect a compensatory process (e.g., Hockey, 1997). For instance, individuals with a low capacity or an inefficient strategy may need to engage additional amounts of effort to achieve a level of performance that is comparable to the performance of individuals with a high capacity or a good strategy (e.g., Smith & Hess, 2015). Therefore, while effort and performance may be correlated in some cases, performance outcomes only provide a limited indication of actual engagement level. This is in part due to the fact that the relationship between effort and performance is not always monotonic. Overall, effort and performance refer to different aspects of action, as suggested by studies reporting a dissociation between attentional effort and performance (see Berry et al., 2017). Thus, MIT theory clearly predicts effort investement rather than performance.

Motivational Intensity Theory

Formulation and Predictions

Initially, Brehm formulated a set of MIT predictions to provide a motivational analysis of goal attractiveness (Brehm, 1975; Brehm et al., 1983). He proposed that the attractiveness or unattractiveness of a goal is a direct function of the level of energy mobilized to attain that goal. The more energy an individual mobilizes in anticipation of a task, the more valuable they should rate a positive outcome and the more unpleasant they should rate a negative outcome, respectively. In accordance with cognitive dissonance theory (Festinger, 1957), individuals should attribute more positive or negative value to goals that require some costs to reduce the dissonance induced by these costs. Therefore, Brehm aimed to predict goal attractiveness from the amount of energization. He conceptualized energization as the "process by which an organism prepares to undertake an effortful task" (Brehm et al., 1983, p. 22). The theory assumes that changes in energization will be anticipatory when changes in *perceived difficulty* are foreseen (e.g., increased energization when a difficult task is imminent or decreased energization when a difficult task is close to its end). Moreover, he associated energization with the anticipation of physiological energy supply, such as blood sugar and oxygen, to the relevant nerve and tissues, but his primary concern was its psychological aspects.

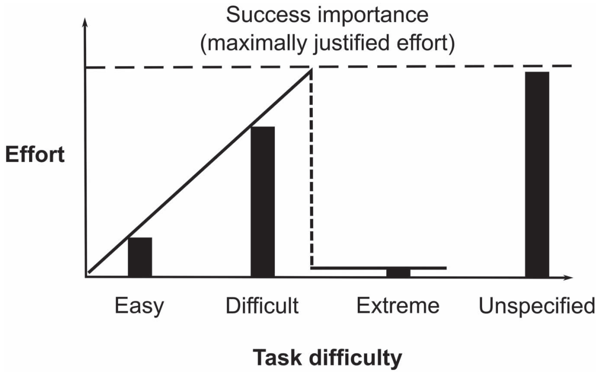
The MIT suggests two major determinants of effort, perceived task difficulty and success importance. The interplay between these two determines how much effort will be mobilized. First, it is worth highlighting that, according to MIT, perceived (subjective) difficulty rather than the objective difficulty of a task should determine effort. Accordingly, effort processes build on the perception of individuals rather than on the task itself. There are different ways of operationalizing task difficulty, such as changing the required level of performance with which participants are asked to perform a task or by changing the task itself—for example, changing the number of elements to be remembered in a working memory task or varying the signal-to-noise ratio in a perceptual discrimination task (Mante et al., 2013; Towse & Hitch, 1995). According to MIT, these task characteristics are expected to influence perceived difficulty, which will determine in turn effort. This makes sense when considering that subjective difficulty might vary across individuals for a given task due to interindividual differences in terms of ability or strategy for instance. Finally, it is of note here that task difficulty is not equivalent to likelihood of success. Within ranges, difficulty can vary without impacting success likelihood, which should become a concern only to the extent that there is appraisal uncertainty regarding task demand or individual capacity. Thus, MIT predicts effort to be determined by subjective difficulty, that is, an individual's expectation about the difficulty of a task rather than directly by the task characteristics.

Second, Brehm conceptualized success importance—that is, the magnitude of motivation determined by needs, rewards, or outcomes—as a *potential* motivation. In contrast, he considered the *actual intensity* of motivation as the amount of effort at one moment in time. This distinction suggests that, when individuals can evaluate the difficulty of a task, potential motivation determines the maximally justified effort. Accordingly, Brehm proposed that it is the purpose of effort to produce instrumental behavior rather than to directly satisfy needs or acquire potential outcomes. In other words, people adapt their effort to attain their goals and effort for instrumental behavior is not simply proportional to needs and/or outcome value. He assumed that the motivational system is constructed so as to conserve energy, which is in line with the resource conservation principle stipulating that individuals avoid wasting resources (e.g., Gibson, 1900). This also complies with the law of least effort postulating that, for a given outcome, individuals tend to prefer the least effortful action (Hull, 1943; Kool et al., 2010). Therefore, effort should not be greater than is necessary to produce the needed instrumental behavior—that is, effort should remain low for an easy task even if task success is of high importance because it only requires low resources to succeed in the task. However, potential motivation determines the upper limit of effort allocated to a task with a given difficulty. If the effort required for a given task difficulty exceeds the level of potential motivation, the theory predicts that individuals disengage from the task. In line with a cost–benefit analysis and the resource conservation principle, people avoid mobilizing resources that are not required by task difficulty or not justified by task importance.

Drawing on these assumptions, the core predictions of MIT stipulate that when task difficulty is clear and known, effort is a function of perceived task difficulty as long as success is possible and required effort is justified by success importance. When the required effort exceeds the level of effort justified by success importance or when the task is perceived as impossible (for instance when the task may only permit the participant to perform at chance level), no effort is expected. Only when task difficulty is unspecified, success importance directly determines effort. These predictions are depicted in Figure 1. Importantly, people may vary in terms of perceived difficulty and drop-off point, that is, the maximum tolerable perceived difficulty level at which people disengage (see also Kukla, 1972). Therefore, the sawtooth function of these predictions should rather look like an inverted U when considering a group of participants. This should also apply to MIT and/or when the tasks and the measures allow averaging across trials.

However, the task difficulty should only impact effort if individuals have enough information about the difficulty of a task. In some cases, individuals may not know the difficulty of a task

Figure 1
Predictions of Motivational Intensity Theory



(*unspecified* task difficulty), perhaps because an individual never performed the task, the task's difficulty varies between trials or because people do not know the performance requirements, for example, how fast they should react. Moreover, in some circumstances, people can choose the difficulty of the task, for instance by determining the standard to be achieved to be successful or in "do-your-best" situations, that is, *unfixed* task difficulty. In these situations, the theory predicts—in line with the resource conservation principle—that individuals will engage effort in proportion to potential motivation, that is, the amount of effort that is justified by success importance. That is, success importance directly determines effort if task difficulty is unspecified. However, whereas this issue is not formally mentioned in the theory, it is fair to suppose that there is an upper limit on how hard a person can try. Therefore, if task difficulty is unspecified, effort should be a function of success importance only until people can try no harder. Beyond this upper effort limit, importance should have no effect.

Cardiovascular Measures of Effort

To overcome the limitations related to self-reports and performance indexes, empirical tests of MIT exploited physiological measures to assess cognitive effort investment. This line of research was initiated by Wright (1996) who integrated the psychophysiological research of Obrist (1976, 1981; Obrist et al., 1978) with MIT. In his studies, Obrist investigated cardiovascular responses during classical conditioning and avoidance paradigms in animals and humans. Most relevant, his research program revealed a systematic increase in β-adrenergic sympathetic activity on the heart when individuals exert control over their default behavior, for example, when actively avoiding a stimulus. Interestingly, Obrist also investigated the impact of task difficulty and found a systematic sympathetic increase only during difficult tasks compared to easy or impossible tasks (Obrist et al., 1978, Study 2). Drawing on these findings, Wright postulated that β-adrenergic sympathetic impact on the heart reflects effort. Accordingly, he tested predictions of MIT based on measures of cardiovascular responses.

It is important to consider here that β-adrenergic sympathetic activity on the heart differentially influences the various cardiovascular parameters for physiological reasons. Heart rate (HR), the number of heartbeats per minute, is influenced by both sympathetic and parasympathetic activity. An increase in HR does not systematically reflect an increase in sympathetic activity but can be attributed to a decrease in parasympathetic activity. The cardiac preejection period (PEP)—the time interval between the onset of ventricular depolarization and the opening of the aortic valve—is the noninvasive parameter that is most influenced by β-adrenergic sympathetic activity. PEP reflects heart contractility, which is almost uniquely determined by sympathetic activity. Moreover, cardiac contractility strongly influences systolic blood pressure (SBP), the maximal blood pressure between two heartbeats. However, HR and diastolic blood pressure (DBP), the minimal pressure between two heartbeats, are commonly assessed together with PEP and SBP. In some cases, they may also respond to sympathetic activity but other factors, such as parasympathetic activity for HR, or peripheral resistance for DBP, may also mask this impact. Therefore, studies testing MIT predictions mainly considered PEP and SBP as primary dependent variables because these two parameters more reliably reflect effort-related β-adrenergic impact on the heart.

The seminal work of Kahneman (1973) on attentional effort also exploited measures of sympathetic activity as cardiovascular reactivity and pupillary responses (Kahneman & Beatty, 1966; see van der Wel & van Steenbergen, 2018, for a review). Recent work indeed showed a relationship between pupil dilation during cognitive performance and neural activity in the locus coeruleus (LC). The LC is the brainstem nucleus releasing noradrenaline, a pure adrenergic sympathetic neurotransmitter and hormone (Joshi et al., 2016). Pupil dilation may thus respond similarly to cardiovascular reactivity in the context of challenging tasks—if it relies on sympathetic activation rather than parasympathetic deactivation (e.g., Bijleveld et al., 2009; Gilzenrat et al., 2010). Importantly, this claim is also consistent with the reinforcement meta-learner (RML) theory described below, which associates LC activity with energization, learning rate, and effort (Silvetti et al., 2018). Therefore, whereas previous studies testing MIT predictions assessed effort as cardiovascular reactivity, it is worth to remind that other measures of sympathetic activity, such as pupillary responses, may provide additional insights into the mechanisms underlying effort.

Supporting Evidence

We will now present empirical findings that supported MIT. We will not provide a complete review of all the studies that tested these predictions, which was done in previous work (see Gendolla & Wright, 2005; Gendolla, Wright, et al., 2012; Richter et al., 2016; Wright & Kirby, 2001, for reviews). Rather, we will focus on representative studies that provided compelling evidence for theoretical assumptions that link MIT to recent models of control allocation.

Richter et al. (2008) tested the nonmonotonic relationship between perceived task difficulty and effort assessed as cardiovascular reactivity (PEP, SBP, DBP, and HR), when task difficulty is known and fixed. Participants started with a resting period allowing the measure of cardiovascular baseline values. Then, they performed an adapted version of the Sternberg task (Sternberg, 1966), where they had to decide whether a target letter was part of a previously presented nonsense series of four letters. Task difficulty was manipulated between participants at four different levels through various presentation times of the nonsense letter series: low (1,000 ms), moderate (550 ms), high (100 ms), or impossible (15 ms). Results revealed that PEP and SBP reactivity increased across the first three difficulty levels and then dropped in the impossible condition. This pattern was not visible on DBP and HR. Together, these findings revealed the expected sawtooth (or inverted-U) pattern of effort allocation as predicted by MIT, assessed as β-adrenergic sympathetic impact on the heart. As expected, this effect was obtained by manipulating task difficulty from an easy up to an impossible condition.

A different study of Gendolla and Richter (2006) investigated the interaction between perceived task difficulty and potential motivation on effort assessed as cardiovascular reactivity (SBP, DBP, and HR). Potential motivation was manipulated through the presence or absence of social observation with the rationale that success importance should increase in the presence of other people when performing a task. After a baseline period, participants received instructions and performed practice trials for an adapted version of the d2 task (Brickenkamp & Zillmer, 1998), where they had to detect a specific combination of letters and apostrophes among distractors. The task was either easy or difficult, which was manipulated through the presentation times of the stimuli, that is, 3,000 ms or 700 ms, respectively. Then, for half of the participants, the experimenter took a seat next to them when they performed the experimental task. In the control condition, participants achieved the task alone. Results revealed stronger SBP and DBP reactivity in the social observation condition when the task was difficult compared to the three other conditions. Cardiovascular reactivity was low in the easy conditions independently of social observation, as well as in the difficult/control condition. Together, these findings indicated that perceived task difficulty interacts with potential motivation to determine effort. If the required effort exceeds the maximally justified effort (potential motivation), then people disengage from the task. In other words, people mobilize resources in difficult tasks only if the required effort is justified by success importance.

Finally, two studies of Richter and Gendolla (2006) sought to examine the impact of potential motivation on effort assessed as cardiovascular reactivity (SBP, DBP, and HR) under unclear task difficulty compared to fixed and known difficulty. Only under unspecified (unclear or unfixed) task difficulty, MIT predicts that potential motivation directly determines effort. After a baseline period, participants could win an attractive poster (Study 1) or a monetary reward (Study 2) when succeeding in a memory task. Task instructions presented either clear or unclear information about task difficulty. Participants were told that they would be presented with successive nonsense series of four letters during 5 min. In the clear difficulty condition, they received information about the exact number of letter series displayed during the task and to be recalled at the end of the task—four series in Study 1 (easy) and 30 in Study 2 (impossible). In contrast, in the unclear condition, they did not know how many letter series they would need to memorize. However, both the clear and unclear conditions included the same number of letter series, which appeared successively on the screen. Results showed for both studies an increase in SBP reactivity when incentive was high and task difficulty unclear. In contrast, SBP reactivity was low when incentive was low or when task difficulty was clear (easy or impossible). DBP followed a similar pattern but was only significant in Study 2. HR followed a similar pattern in Study 2 but was not significant in both studies. Together, these findings supported the prediction of MIT that potential motivation directly determines effort only when task difficulty is unspecified.

Numerous other studies draw on MIT to investigate the impact of various variables on perceived task difficulty and success importance. For instance, studies investigated ability beliefs (see Wright, 1998), experienced fatigue (see Wright & Stewart, 2012), mood states (see Gendolla, Brinkmann, & Silvestrini, 2012), implicit affect (e.g., Gendolla, 2012; Gendolla & Silvestrini, 2011), pain (Cancela & Silvestrini, 2021; Silvestrini, 2015, 2018), depressive symptoms (e.g., Brinkmann & Gendolla, 2007, 2008), or self-involvement (Gendolla & Richter, 2010). While physiological evidence in support of MIT prediction is ample, the neurocognitive processes underlying effort allocation mechanisms remain unclear. In the next sections, we discuss three models that offer insights into these neurocognitive mechanisms from a computational, neurobiological, and neuronal perspective.

The EVC Theory

Formulation

In the last decades, a variety of studies examined the neural and computational mechanisms by which people *execute* cognitive control over their information processing. These efforts focused on elucidating the *implementation* of control. However, less is known about the decision processes underlying the *allocation* of control, that is, how people decide how much control to allocate among tasks. EVC theory proposes that individuals carry out this decision by weighing the potential benefits of allocating control against associated costs and then selecting the type and amount of control with the greatest expected future value (Shenhav et al., 2013). According to EVC, control allocation concerns the selection between control signal *identities* (e.g., which tasks to perform or which cognitive processing mechanism to invoke), as well as the specification of a control signal *intensity* (e.g., how much control to allocate to a particular task). Formally, it is assumed that participants exert the control signal that maximizes the EVC,

$$\text{signal}* \leftarrow \text{argmax}_i\,[\text{EVC}\,(\text{signal}_i, \text{state})]. \tag{1}$$

The EVC of any candidate control signal is contingent on the current situation (e.g., situational variables, such as expected task environment or internal motivational state) and determined by summing expected values over all possible outcomes and subtracting the cost associated with a given control signal intensity. As described in Shenhav et al. (2013), the EVC of a candidate control signal amounts to

$$\text{EVC}\,(\text{signal}, \text{state}) = \Big[\sum_i \Pr\,(\text{outcome}_i|\text{signal}, \text{state}) \cdot \text{Value}\,(\text{outcome}) - \text{Cost}\,(\text{signal})\Big], \tag{2}$$

where the expected probability (Pr) of each outcome is a function of the candidate control signal, as well as the expected state of the task environment. The value incorporates both immediate and future rewards associated with a given outcome. The cost may take different functional forms but is assumed to scale monotonically with the intensity of the control signal.[2]

---

[2] The cost may attach to other terms, such as the change in control signal from the last time step to the current time step, reflecting a reconfiguration cost (Musslick et al., 2015).

While Shenhav and colleagues introduced EVC theory as an integrative perspective of dACC function, recent simulation work highlights virtues of the theory in explaining various behavioral phenomena in cognitive control tasks, such as the Stroop effect or task performance in cued and voluntary task switching (Lieder et al., 2018; Musslick et al., 2015, 2019). Furthermore, EVC theory has been successfully applied to inform the relationship between behavioral and neural correlates of incentive evaluation (Frömer et al., 2021) and attentional allocation (Shenhav et al., 2018). One noteworthy contribution of EVC theory is a formal distinction between control allocation and control implementation. The former concerns the decision about how much control to allocate to which tasks based on motivational factors, such as expected task difficulty or reward; the latter concerns the process of exerting control. This distinction leads researchers to suggest that low performance in control-demanding task may result from motivational factors, such as distorted expectancy of certain outcomes or a low sensitivity to reward, rather than just a limited capacity to implement control (Frömer et al., 2021; Grahek et al., 2020; Musslick, Cohen, et al., 2018; Musslick et al., 2019). This may help reveal the computational mechanisms underlying dysfunctions of cognitive control as observed in various psychiatric disorders, such as depression (Grahek et al., 2019).

Supporting Evidence and Explanatory Scope

A central proposition of EVC theory pertains to the attribution of control allocation to dACC function. Here, we refer the interested reader to Shenhav et al. (2013) for an extensive review of neural evidence and mechanisms and focus instead on the behavioral phenomena in support of the computational mechanisms underlying EVC theory (Musslick et al., 2015). The theory suggests that individuals engage in a cost–benefit analysis to decide about the amount and type of control to allocate. As a consequence, the theory lends itself to explaining phenomena at the intersection of cognitive control and motivation.

A core behavioral prediction is that the cost of allocating cognitive control can be offset by reward, leading to performance improvements on a task. Padmala and Pessoa (2011) demonstrated the effects of incentives on performance in a picture-word Stroop task. Their task required participants to categorize a picture (either a house or a building) while ignoring a superimposed strings of letters which were either congruent, incongruent, or neutral with respect to the picture (“HOUSE,” “BLDNG,” or the neutral stimulus “XXXXX”). Each stimulus was preceded by a cue, signaling the participants whether their performance on the next trial could yield a monetary reward or not. As predicted by EVC theory, the prospect of reward improved the participants’ performance on incongruent trials (e.g., the picture of a house superimposed by the word “BLDNG”) relative to neutral trials (e.g., the picture of a house covered by the letters “XXXXX”), suggesting reduced interference from the word distractor. At the same time, incentivized trials reduced the facilitation of a response on congruent trials (e.g., the picture of a house superimposed by the word “HOUSE”) relative to neutral trials. This reward-induced reduction of both distractor interference and facilitation aligns with a central proposition of EVC theory, namely that reward can offset the costs of allocating control to a task (e.g., picture-categorization), leading to a narrowing of attention toward the task-relevant stimulus. The compensatory effect of reward can extend to other forms of costs, such as performance costs associated with task switching. As predicted by the EVC model (Musslick et al., 2015), and demonstrated by Umemoto and Holroyd (2015), participant’s ability to switch between tasks can be improved by associating the performance of a task with reward, yielding lower task switch costs in terms of both reaction times and accuracy.

Incentives have also been shown to impact task choice. As stated in the previous section, EVC theory postulates that control allocation encompasses a selection of both control signal intensity (i.e., the amount of control allocated to a task) and control signal identity (e.g., which control mechanism to engage or which task to perform). The latter implies that higher incentives can drive participants to select a task, even if the task is associated with a higher cognitive demand compared to an alternative task. Westbrook and Braver (2015) devised a cognitive effort discounting (COGED) paradigm in which participants can choose, on each trial, whether they want to perform a baseline task with low cognitive demand for a low reward or whether they want to engage in an alternative task with a high cognitive demand for a higher reward. The amount of reward offered for the baseline task is adjusted trial-by-trial to identify the point of indifference, that is, the reward at which participants are indifferent between performing the low-demand baseline task and performing the high-demand task. This procedure can be used to quantify, for each participant, the subjective value of performing a task with certain cognitive demand. A computational model of EVC theory replicates the behavior of human participants in this task, showing that the subjective value of a task decreases with its difficulty (Musslick et al., 2019). However, analyses of the EVC model show that such measures may not be ideal for characterizing individual differences in the cost of cognitive control since measures of performance and choice can be confounded by other information processing factors, such as one’s efficacy of implementing cognitive control or a person’s automaticity on a task (Grahek et al., 2020; Musslick, Cohen, et al., 2018; Musslick et al., 2019). The analytical insights offered by EVC theory are also helpful for illuminating relationships between latent variables in earlier theories of effort allocation, such as MIT.

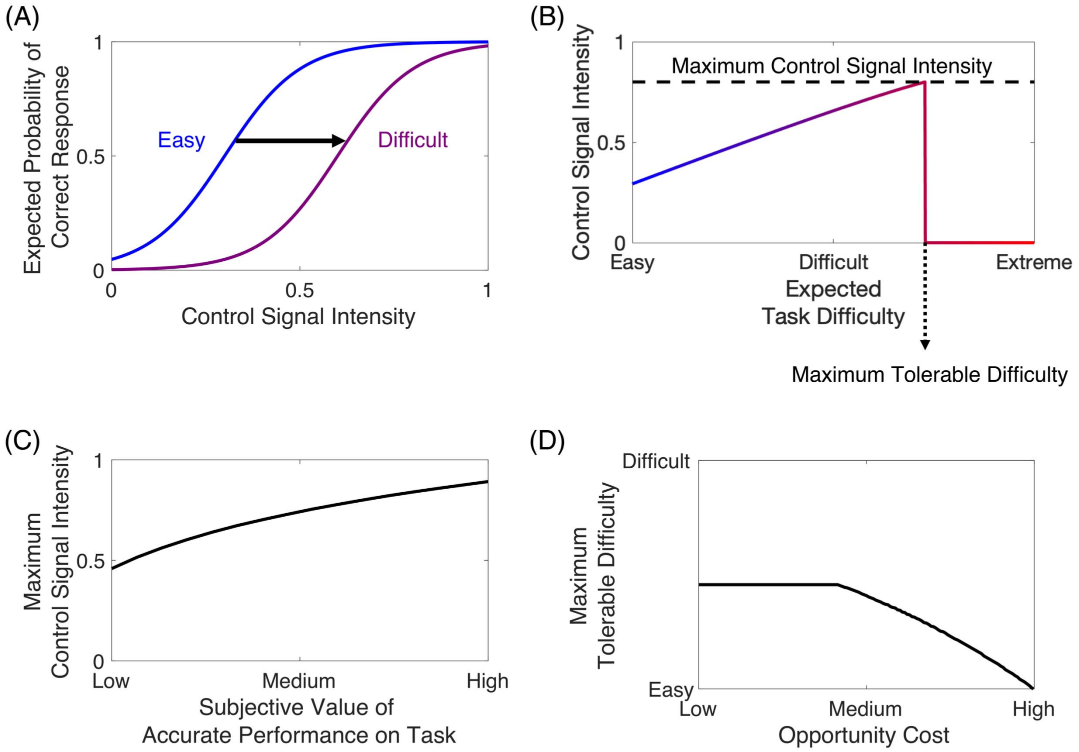
Relationship to MIT

Before comparing predictions between EVC theory and MIT, it is worth examining important differences in terminology. Brehm et al. (1983) conceptualized the intensity of motivation as a function of perceived task difficulty and success importance. In EVC theory, the intensity of motivation can be formalized as the amount of cognitive control allocated to a task. As in MIT, it is a function of the task’s difficulty, as well as the needs, rewards, and outcomes associated with exercising control.

Previous instantiations of EVC theory quantify perceived task difficulty as the expected probability of performing accurately on a task for a fixed amount of control (see Figure 2A; Musslick et al., 2015; Musslick, Cohen, & Shenhav, 2018; Musslick et al., 2019). It is worth highlighting that these instantiations apply a more narrow definition of perceived task difficulty than the one used in MIT. In EVC theory, perceived difficulty depends on the characteristics of the task, as well as an individual’s experience with the task, all of which can be summarized as the expected probability (Pr) of responding correctly on the task. In MIT, perceived difficulty may also depend on performance standards, that is, how many

Figure 2

Predictions of Expected Value of Control Theory



Note. (A) The expected probability of a correct response Pr(correct) to a task can be modeled as a logistic function of control signal intensity. The expected difficulty of a task can be operationalized as the bias of the logistic function: the more difficult the task, the more control is needed to yield the same probability of responding correctly (black arrow). Conversely, the same amount of control (e.g., 0.5) yields lower accuracy on a difficult task than on an easy task. (B) Optimal control signal intensity as a function of task difficulty. Warmer colors indicate a higher task difficulty. The dashed horizontal line plots the highest control signal intensity allocated across all levels of task difficulty. The dashed vertical arrow marks the highest task difficulty at which the EVC agent is willing to invest control. (C) The maximum worthwhile control intensity as a function of the subjective value V(correct) of performing the task correctly. (D) The maximum tolerable difficulty as a function of the subjective value of performing an alternative task (opportunity cost). EVC = expected value of control. See the online article for the color version of this figure.

correct answers a participant should provide to succeed in a task. EVC conceptualizes the latter in terms of a desired performance outcome that is associated with a given value. For instance, if the task demands a high performance standard (e.g., reward is only paid if an individual's accuracy is above 90%), then EVC assumes a high *Value(accuracy > 90%)* associated with high performance outcomes (greater than 90% accuracy) and a low *Value(accuracy ≤ 90%)* associated with low performance outcomes (equal or less than 90% accuracy). As we will show below, the subjective value of a task determines, among other variables, the maximum amount of control that an agent would be willing to invest or, in the terminology of MIT, its potential motivation (success importance).

According to MIT, it is the purpose of effort to facilitate instrumental behavior, that is, to attain a given goal. In EVC theory, this corresponds to reaching a desired outcome (e.g., performing 90% correctly on a task). The *attractiveness* of a goal is conceptualized as a function of the amount of energy (control intensity) mobilized to attain a goal and can thus be formalized as the expected value of implementing the optimal control signal in a given environment, *EVC(signal*, state)*. Similar to MIT, EVC theory assumes that the system conserves control (energy) by weighing the benefits of exerting control against an intrinsic *Cost(signal)*. Effort is not necessarily assumed to be limited but, in effect, constrained by a cost function. This is consistent with the resource conservation principle which is embedded in MIT and states that people avoid spending unnecessary or unjustified effort.[3] Finally, both MIT and EVC assume that effort and performance can be dissociated. The latter applies to situations in which increases in effort have little effect on performance, for example, when applying small amount of control in difficult tasks (cf. Figure 2A).

MIT makes two crucial predictions about the relationship between invested effort and task difficulty. First, the amount of

---

[3] Note that neither EVC nor MIT provides a rationale for the resource conservation principle. Some have suggested that a cost of control results from computational dilemmas in neural systems (Musslick et al., 2017; Musslick, Jang, et al., 2018; Musslick & Cohen, 2021; Zénon et al., 2019) whereas others have suggested that such costs originate from biological constraints (e.g., Holroyd, 2016).

effort is assumed to scale with the difficulty of a task in a nonmonotonic fashion. That is, the amount of effort may increase with the difficulty of a task until the task reaches a certain level of difficulty. We refer to this drop-off point as the *maximum tolerable difficulty*. If the task surpasses the maximum tolerable difficulty, the agent may avoid allocating effort to the task. Figure 2B illustrates that this prediction is shared by EVC theory: The amount of control invested increases until a maximum tolerable task difficulty is reached and drops sharply if the task becomes more difficult (see Supplemental Material for simulation details; the code for these simulations is available at https://github.com/musslick/MIT_EVC). Note that the simulated EVC agent reaches its highest control signal intensity that is worth allocating (i.e., success importance) at maximum tolerable difficulty. Thus, MIT and EVC theory make similar predictions about the nonmonotonic relationship between effort investment and task difficulty.

A second crucial prediction made by MIT regards situations in which task difficulty remains unknown (unspecified) or where it can be determined by participants themselves (unfixed). In such cases, MIT predicts that the amount of allocated effort corresponds to success importance or, in EVC terminology, to the maximum control intensity that is worth allocating across all task difficulties (maximum worthwhile control intensity), $\max_{\text{task difficulty}}(\text{signal}*)$. However, EVC theory suggests that this may not always be the case. EVC theory assumes that the allocated amount of control depends on the expected state of the environment, including the expected difficulty of the task to be performed. Even if a task is unknown to the participant, they may have a prior about its difficulty. Thus, if the difficulty of a task remains unspecified, the amount of control allocated depends on a participant's expectation of the task's difficulty. In such circumstances, EVC theory predicts that a person would allocate their maximum worthwhile control intensity for a task only if their expectation about the task's difficulty matches the maximum tolerable difficulty for that task.[4] Otherwise, if the task difficulty remains unspecified, an individual is predicted to allocate the amount of control that corresponds to their expectation of task difficulty. That is, if a person expects the task's difficulty to be intolerable, then they may decide to not allocate effort to the task at all, independent of the task's actual difficulty. A different scenario arises if the task's difficulty can be determined by the person itself. Without any additional incentives (e.g., by instructing participants to do their best), EVC theory predicts that participants would choose to select the lowest task difficulty yielding a maximum EVC (see Figure S1).[5] However, in this situation, the *amount* of cognitive control allocated to that task would still be determined by motivational factors such as the value of performing the task correctly, the expected difficulty of the task, as well as the costs of allocating control.

The conceptual similarities between EVC theory and MIT suggest that the former can be leveraged to gain formal insights about the latter. For instance, Figure 2C shows that the maximum worthwhile control intensity (success importance) scales with the subjective value of performing the task correctly, as already suggested by Brehm et al. (1983). In addition, EVC theory reveals dependencies that are not explicitly stated in MIT. For instance, the maximum tolerable difficulty of a task is predicted to be a function of opportunity costs: Simulated EVC agents become more likely to disengage from the primary task if the subjective value of the next best alternative task increases (Figure 2D). Moreover, as shown in Figure S2A, success importance, operationalized as maximum worthwhile control intensity, decreases with the cost of allocating cognitive control. Overall, these results suggest that EVC theory can be leveraged as an analytic framework for quantifying the relationship between defining variables of MIT.[6] Note that the EVC framework, as stated in its original form (Shenhav et al., 2013), should be regarded as a theoretical framework, not a model. That is, it provides theoretical constraints for deriving models of effort allocation building on the formulation of a cost–benefit trade-off. For instance, different models of EVC theory (e.g., the model depicted in Figure 2) may entail different instances of cost functions leading to different, testable predictions. Furthermore, while EVC theory formally describes the decision-making processes underlying the allocation of cognitive control, it is also not constrained to a particular neurobiological implementation of those mechanisms (but see Shenhav et al., 2013, for a review of putative neural correlates). In the next section, we present a biologically inspired model which shares similarities with MIT and EVC theory and proposes a RML mechanism for learning how much effort to allocate.

The RML Model

Formulation

Theories of effort and control allocation share one key tenet: exerting effort is costly. Allocation of resources should be optimized to achieve best possible positive outcomes while minimizing the cost. Hence, the value of allocating resources equals potential reward minus the cost. While from the cognitive point of view this is a plausible assumption, few theories have characterized the adaptive mechanism underlying this computation, and its neural correlates. Optimizing effort allocation requires estimating expected reward, the required cost attached to it, and updating such estimates on the go based on actual experience. Silvetti and colleagues proposed a novel framework, the RML theory (Silvetti et al., 2018), which models this optimization process. RML is a reinforcement learning agent designed to learn autonomously to optimize effort allocation (when it is valuable to exert effort and how much). This agent is built in a neurobiologically plausible manner. Its architecture reproduces neural systems known to play a critical role in the emergence of adaptive resource allocation: the dACC and the ascending neuromodulatory systems (dopamine and noradrenaline).

Dopamine (released by the ventral tegmental area [VTA]) broadcasts reward and prediction error signals to dACC (Schultz et al., 1997). Noradrenaline (released by the LC) broadcasts, among others, signals about how changeable the environment is to dACC (environmental volatility, Behrens et al., 2007; Silvetti, Seurinck, & Verguts, 2013). These teaching signals are essential to update predictions about the world. The dACC is thought to implement this update mechanism. Indeed, dACC is more active when we make errors (Holroyd et al., 2004; Iannaccone et al., 2015), when

---

[4] This assumes that the person has accurate expectations about other aspects of the environment (e.g., rewards associated with performing accurately on the task), as well as their own control parameters (e.g., the cost of allocating control).

[5] This precludes instances in which individuals seek to exert cognitive effort (see Inzlicht et al., 2018).

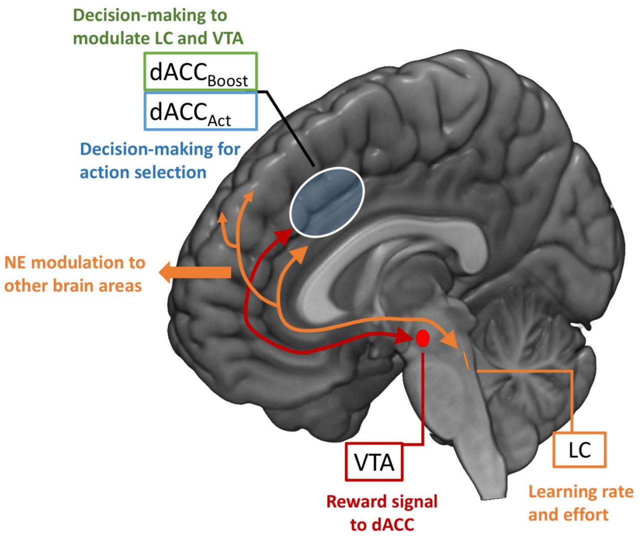
[6] The interested reader may refer a computational implementation of EVC theory for framing predictions in terms of MIT: https://github.com/musslick/MIT_EVC.

unexpected events occur and when outcomes are better or worse than expected (Alexander & Brown, 2011; Jessup et al., 2010; Vassena, Krebs, et al., 2014). Critically, dACC activity also increases when we expect to perform difficult tasks (Vassena, Silvetti, et al., 2014), as well as during execution of demanding tasks, and is implicated in effort-reward trade-offs during decision-making (Klein-Flügge et al., 2016). These findings from multiple research lines inspired the RML theory, which implements dACC as an integrator of predictions with brainstem teaching signals (noradrenaline and dopamine). Dopamine is known to be involved in decision-making, cost–benefit trade-offs, learning, and flexibility (Cools, 2019; Salamone et al., 2015). Noradrenaline has been implicated in energization of behavior (Varazzani et al., 2015), increase in neural gain (Gilzenrat et al., 2010; Mather et al., 2016), surprise, and volatility (Preuschoff et al., 2011; Silvetti, Seurinck, & van Bochove, et al., 2013).

The key innovation modeled in the RML is the cortico-brainstem recursive loop (Figure 3): neuromodulatory brainstem signals train dACC activity, which in turn can up- or downregulate brainstem signals depending on contextual needs. This top-down regulatory capacity implies the ability to tune reward signals also in the absence of immediate reward (as is the case for higher order conditioning or delay discounting, when a reward is expected but only in the future, and the agent needs to keep pursuing a goal). Similarly, it allows tuning the strength of the noradrenergic release for adaptive resource allocation (aimed at energizing behavior via increase of neural gain in task-relevant brain areas). Thus, the RML implements optimal resource allocation along two key dimensions: selecting which are the best actions to be performed (toward the environment) and selecting whether it is worth boosting noradrenaline and dopamine release to achieve the goal (modulating its internal parameters, i.e., meta-learning).

Figure 3

The Reinforcement Meta-Learner (RML): Model Architecture and Neurobiological Implementation (Adapted From Silvetti et al., 2018)



Note. VTA broadcasts reward and prediction signals to dACC, which in turn can regulate dopaminergic release (red pathway). LC broadcasts learning signals about environmental volatility to dACC, which in turn can regulate noradrenergic release to support effortful behavior (orange pathway). dACC performs two key computations: action selection toward the environment (dACC_{Act}) and regulation of the system's internal parameters (meta-learning, $\text{dACC}_{\text{Boost}}$). Both computations can be seen as decisions, results of a cost–benefit trade-off. VTA = ventral tegmental area; LC = locus coeruleus; dACC = dorsal anterior cingulate cortex; NE = norepinephrine (noradrenaline). See the online article for the color version of this figure.

Supporting Evidence and Explanatory Scope

The RML model is a RML agent that simulates neural activity in dACC and neuromodulatory nuclei (VTA, LC) and the interactions between these areas. Importantly, it also simulates behavior deriving from such circuit dynamics (see Silvetti et al., 2018 for implementation and mathematical details). The strength of this approach is that RML's architecture is inspired by previous knowledge on this circuit (from animal and human studies), resulting in an agent whose (simulated) neural activity and behavior can be tested against those of actual human participants. This type of model can be considered valid if its complex dynamics capture a wide range of neural and behavioral effects *across different tasks, species, and modalities*. In this sense, RML is not a model of effort allocation per se. Rather, it is a model of a neurobiological adaptive learning systems, whose functions include adaptive effort allocation. To this end, it is important to note that RML has been successfully validated across a series of different tasks and experimental modalities (behavior, fMRI-BOLD activity, and single-cell recordings, see Silvetti et al., 2018).

In terms of explanatory scope, RML captures adaptive control of learning rate (i.e., how quickly we adapt our expectations when things change in the environment), higher order conditioning (i.e., ability to pursue long-term reward requiring several actions to obtain), and allocation of physical and cognitive effort (see Silvetti et al., 2018 for a detailed description of the simulations). Through these mechanisms, RML can learn when it is better to change one's decision strategy because the environment has become more volatile, or when it is worth to pursue a long-term reward even though immediate actions are not rewarded. Although not directly related to MIT, these aspects clearly play a role in daily life decisions about effort investment. Adaptive allocation of cognitive and physical effort emerges from the bidirectional interaction between noradrenaline, dopamine, and the dACC.

The pivotal role of mesolimbic dopamine and VTA, noradrenaline, and dACC in effort-based decision-making is rather established (Chong et al., 2017; Klein-Flügge et al., 2016; Salamone et al., 2015; Vassena, Holroyd, et al., 2017; Vassena, Silvetti, et al., 2014; Walton et al., 2009). The neurocomputational mechanisms were however less clear. The meta-learning dynamics implemented in the RML successfully capture behavior and neural activity in healthy and dopamine-lesioned agents. The RML is able to learn that exerting effort can be valuable when available reward is high and boosts internal catecholamine release to implement effortful actions. However, when the system is impaired, due for example to a dopamine depletion, this dynamic is disrupted. The "healthy" RML generally chooses to perform the hard task for large reward, as animals do. When dopamine is depleted, RML becomes more effort avoidant, engaging less in high effort for high reward option, and refusing to engage at all in a substantial proportion of trials, again similar to human and animal behavior (Silvetti et al., 2018; Walton et al., 2009).

These simulations of brain and behavioral activity are implemented by administering an effort-based decision-making task to the RML. Like an animal, the RML is exposed to several trials, with different difficulty levels. Difficulty is implemented as a function of success rate, which corresponds to changes in the task itself (simulating, e.g., varying difficulty levels of a calculation task or a working memory task). RML learns that boosting catecholamine release (i.e., mobilizing effort) increases success rate on hard trials, yet is not useful (in fact unnecessarily costly) on easy trials. This way, RML learns how to adaptively allocate effort when this can be beneficial.

Relationship to MIT

To exemplify the parallel with MIT and EVC theory, here we describe two novel simulations of two hypothetical scenarios based on previous empirical work (Vassena, Deraeve, et al., 2017; Vassena et al., 2019; Vassena, Silvetti, et al., 2014; the code for these simulations is available upon request). The first is a difficult yet feasible task, featuring four possible difficulty levels, from very easy to very hard. The second is an unfeasible task, featuring four possible difficulty levels, from medium to impossible. In both cases, for each trial, the agent can earn a small or a large reward upon successful completion of the trial. Note that these simulations were run with the same parameter set and architecture as in our published work (see Silvetti et al., 2018 for a detailed description of the mathematical formalization). When confronted with these tasks, RML learns to choose between available options based on the estimation of expected reward and on the cost tied to the required effort, in terms of catecholaminergic boost necessary to successfully complete the task. This is where the meta-learning aspect is critical: the internal boosting signal is necessary to engage in hard tasks, but is also costly, and this cost is factored in into the net-value computation. This net value measured in RML-dACC modules fits with previously observed net-value signal coding in dACC (Chong et al., 2017). For example, the net-value signal in the RML-dACC modules is lower for a hard task compared to an easy task when reward is high (Silvetti et al., 2018).

In practice, this means that when a task is easy, more boosting is not necessary. When difficulty increases, more boosting is required to successfully complete the task. This is in line with the key assumption of MIT theory on effort mobilization rising as a function of task difficulty. However, boosting is costly and will only be done when the expected reward is worth it as well as sufficiently likely. This reflects a key proposition of MIT discussed above, that the required effort is mobilized only if it is justified by success importance. The impact of expected reward (small vs. large) is evident in Simulation 1 (Figure 4):[7] when the task is hard but leads to a large reward, the boosting signal measured in the RML-dACC module increases, as well as the consequent probability of engaging in the task. However, when the reward is low, both probability to engage and boosting signal drop. Simply put, it is not worth the effort. Simulation 2 displays the scenario when difficulty is substantially increased, including very hard and impossible difficult situations. In this case, the decision is shifted from "what is worth" to "what is possible." When the task is hard, it is worth engaging in it (and boosting for it). When the task is very hard, it is worth engaging in it (and boosting for it) only if the reward is high. When the task becomes impossible, boosting would not help at all and this leads the agent to disengage. The inverted U-shaped profile of the RML-dACC boosting signal clearly shows that increasing difficulty leads to increase effort allocation up to the point when it is either not worth it, or not possible, when boosting drops. This is fully in line with MIT predictions when considering that the sawtooth pattern of MIT predictions should lead to an inverted-U pattern for a group of (simulated) participants.

The RML belongs to a class of computational neuroscience approaches to learning and adaptive behavior, which combine reinforcement learning models with neurobiological findings (Silvetti et al., 2014). Although developed independently, the links with the psychological view provided by the MIT theory are striking. MIT originally postulates that goal attractiveness is tightly related to the effort mobilized to obtain such goal (i.e., a reward obtained with effort will be perceived as more pleasant). The RML captures this prediction in two ways. First, success is generally less likely on difficult trials, and therefore performing correctly and obtaining a reward on such trials is unexpected from a monitoring perspective (i.e., less likely, and thus more surprising). This results in a positive prediction error (known to be associated with increased dACC activity, Vassena, Silvetti, et al., 2014, 2017) and elicits positive affect (Schouppe et al., 2015; Silvetti et al., 2011). Second, effort mobilization in the RML is associated with top-down boosting of both noradrenaline and dopamine. This boosting triggers increased—internally generated—VTA activity when a reward is obtained with effort, plausibly in line with the subjective experience of increased pleasantness for goals obtained with effort proposed by MIT.

Further, MIT theory substantiates the willingness to mobilize effort in a task as the interplay between perceived difficulty and success importance, hereby defining potential motivation as the maximally justified effort. This mechanism nicely aligns with the core integrative computation performed within the RML-dACC module, where cost of exerting effort is traded off against the expected reward. This computation naturally reproduces the non-monotonic relationship between perceived difficulty and task engagement (see Figure 4). Interestingly, perceived difficulty is not directly implemented in the RML. The model behaves like an animal exploring its environment. In a given experimental task, RML will learn task difficulty by trying out the task, experiencing the outcome (a reward receipt or not), succeeding and failing, thus learning when exerting effort is beneficial, and when it is worthless. This is a trial-and-error optimization procedure that determines subsequent decisions. For example, when a reward is too small, obtained with a large effort, next time in the same conditions RML will refuse to engage. Similarly, if the probability of success is too small (as previously learned), effort will not be mobilized (Figure 4D).

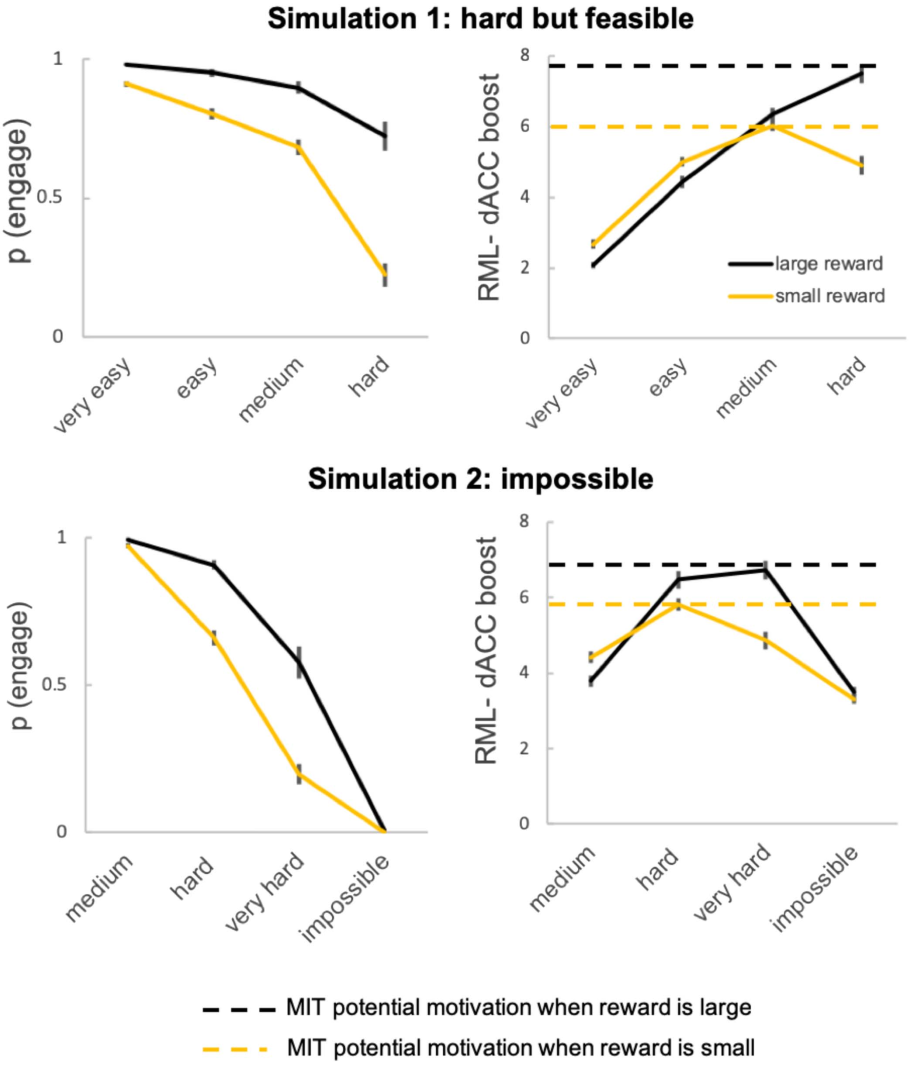
While the RML framework provides a neurobiological and functional architecture for adaptive behavior more generally, the part implementing effort optimization is compatible with the cognitive machinery proposed by the EVC theory. dACC units in the RML integrate reward and cost information, to determine which actions are worth pursuing. Expected reward is factored in this calculation, predicting increased likelihood of exerting effort when attainable reward is large, in line with key tenet of MIT that effort allocation depends on success importance (potential motivation). In

---

[7] Code is available upon request.

Figure 4

Simulations From the Reinforcement Meta-Learner (RML) Model



Note. RML behavior (left panels) and boosting signal in dACC (right panel) in an effort-based decision-making task in two possible scenarios: when the task is hard but feasible (upper row, Simulation 1), and when the task becomes impossible (lower row, Simulation 2). The error bars indicate the standard error of the mean of 23 simulated participants. In each scenario, a small (orange) and large (black) reward condition are represented. The dashed lines indicate potential motivation in MIT terms, that is, the maximally justified effort, which depends here on reward (again orange and black). RML = reinforcement meta-learner; dACC = dorsal anterior cingulate cortex; MIT = motivational intensity theory. See the online article for the color version of this figure.

this integration process, the meta-learning aspect—implemented through cortico-brainstem loops—is critical: the "value" as well as the "cost" of each behavior is calculated through a learning process. This implies that when difficulty is unspecified, the amount of effort exerted will solely depend on the reward at stake, also in line with MIT. Through learning, however, this can be updated, depending on actual rewards obtained from the environment. In terms of model predictions, RML-dACC activity profile resembles an inverted-U: predicted activity increases as a function of expected effort (because of the necessary boost) but only when it is worth it (when the available reward is large enough, see Figure 4).

From a physiological point of view, effort allocation in the RML is implemented as a top-down increase in catecholaminergic release, and particularly noradrenaline, which implies sympathetic activation. Effort as defined by MIT is most often operationalized as cardiovascular reactivity, also a measure of sympathetic activation. Hence, dACC-driven meta-control of catecholamine release is a plausible neural mechanism for determining the amount of effort given perceived task difficulty and/or success importance and triggering the physiological changes necessary to implement such effort, of which increased cardiovascular reactivity is the peripheral read out (Silvestrini, 2017). Converging evidence comes from a recent study showing that pupil dilation, considered a peripheral read out of sympathetic activation driven by noradrenaline release, also follows a similar U-shaped pattern (increasing as a function of difficulty), yet decreasing when the task becomes impossible (Granholm et al., 2017; see also da Silva Castanheira et al., 2021).

Overall, the cortico-subcortical dynamics implemented in the RML capture control of learning rate, higher order conditioning, and adaptive effort allocation with the same neurocomputational machinery and same parameter set (see Silvetti et al., 2018 for extensive explanation of the mathematical modeling). Thus, the key strengths of the RML framework are the neurobiological plausibility of its architecture, the explanatory scope, the adaptive learning aspect, and the fact that it captures neuromodulatory dynamics (Silvetti et al., 2019).

The NMAE

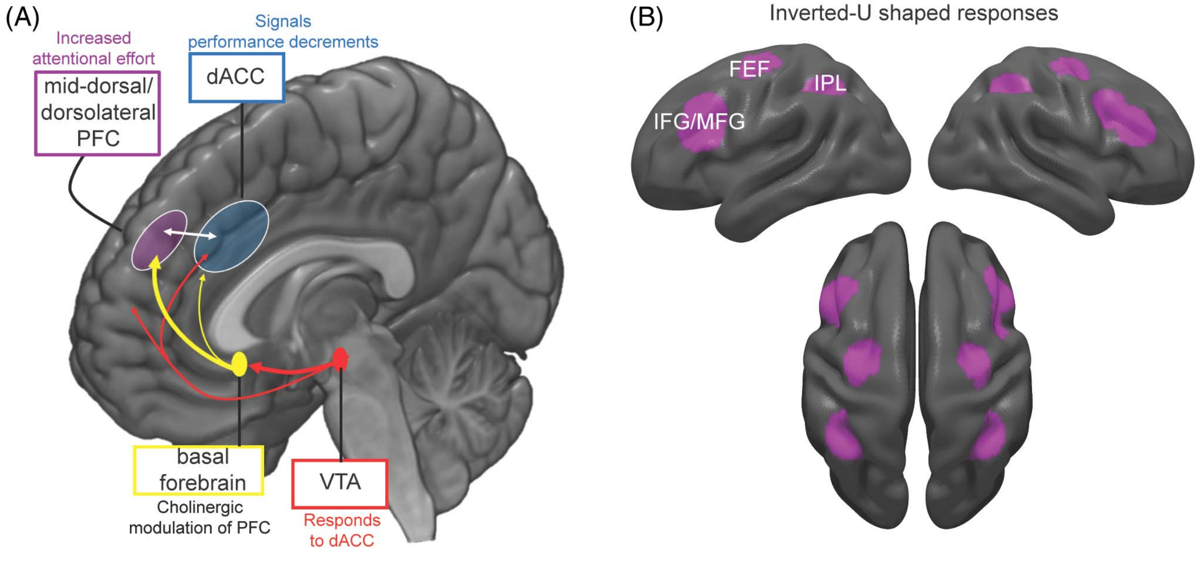
Formulation

The NMAE put forth by Sarter et al. (2006) emphasizes interactions between cholinergic forebrain, dopaminergic midbrain, and prefrontal cortex (PFC) in the implementation of effort. The NMAE posits that effort is elevated in response to the perception of cognitive challenge and/or performance decrements (Sarter et al., 2006). This perception of cognitive challenge may be due to external factors such as the presentation of a distractor, evidence of performance decrements via feedback, or internal factors such as fatigue. Here, increases in attentional effort are defined as the motivated activation of attentional systems to strengthen task-set representations in the face of perceived challenge (e.g., Sarter et al., 2006). Error detection and reward loss monitored by PFC activate attentional systems through a two-step process (Figure 5). First, dACC increases activity within the mesolimbic dopaminergic system (St. Peters et al., 2011). Second, mesolimbic projections to the basal forebrain modulate cholinergic projections to PFC and posterior sensory regions (see Sarter et al., 2016, for recent review) that directly support the maintenance of optimal performance via modification of receptive field properties, distractor suppression, signal detection, enhancement of task representations, etc.

The NMAE framework does not explicitly provide a computational account of the decision process leading to the activation of the dopaminergic system (though see Sarter et al., 2014, for discussion of a role of PFC acetylcholine in reducing opportunity cost). However, similar to EVC, it suggests a monitoring mechanism based on the expected state of the environment, influencing the amount of attentional effort allocated. Furthermore, in contrast to RML, NMAE is agnostic to cost thresholds or parameters contributing to a "decision" to activate the dopaminergic system. NMAE's focus is on the neural mechanisms central to the sustained implementation of effort, which it specifies as involving cholinergic inputs to PFC (as opposed to noradrenergic as specified by RML). However, the RML and NMAE are not mutually exclusive, as the noradrenaline-producing LC projects directly to the acetylcholine-producing basal forebrain (Samuels & Szabadi, 2008). Thus, noradrenergic and cholinergic contributions may occur in parallel or interactively. Future research on the

Figure 5

Neuronal Model of Attentional Effort Highlights a Role of Acetylcholine in Effort



Note. (A) Motivated increases in attentional effort are mediated by dopamine-acetylcholine interactions. In response to performance decrements, dorsal anterior cingulate cortex (dACC) increases the firing of VTA dopaminergic inputs to basal forebrain. Dopaminergic modulation of basal forebrain increases activity of cholinergic inputs to frontoparietal attentional control regions to stabilize performance. fMRI activation in mid-dorsal/dorsolateral PFC tracks increases in attentional effort. (B) Human fMRI studies show empirical support for U-shaped patterns of brain activity in response to increasing task difficulty. Frontoparietal regions demonstrating consistent quadratic effects include bilateral inferior frontal gyrus and middle frontal gyrus (IFG/MFG), frontal eye fields (FEF), and inferior parietal lobule (Callicott et al., 1999; Linden et al., 2003; Van Snellenberg et al., 2015). dACC = dorsal anterior cingulate cortex; VTA = ventral tegmental area; PFC = prefrontal cortex; fMRI = functional magnetic resonance imaging. See the online article for the color version of this figure.

NMAE incorporating monitoring of noradrenergic activity is warranted.

Supporting Evidence and Explanatory Scope

The neuromodulator acetylcholine has been implicated in models of attention since early studies demonstrating modest attention enhancing effects of nicotine, which acts on nicotinic acetylcholine receptors (nAChR; for review, see Demeter & Sarter, 2013; Heishman et al., 1994; Sarter et al., 2009). Building on precisely targeted pharmacological effects on alpha4beta2* nAChR, lesion studies and in vivo measurement of cholinergic activity have firmly established the importance and necessity of the cholinergic input system for attention (e.g., Deco & Thiele, 2009; Giocomo & Hasselmo, 2007; Hasselmo & Sarter, 2011; McGaughy et al., 1996; Muir et al., 1994; Robbins et al., 1989; Sarter & Parikh, 2005).

This neuronal model was developed based on a body of attentional control research in rodent models which demonstrated a critical role of cholinergic inputs to right medial PFC for attentional performance using the Sustained Attention Task distraction condition (dSAT; Sarter & Lustig, 2020). The dSAT was adapted for use in humans, and a series of functional magnetic resonance imaging (fMRI) studies have indicated a specific role of right mid-dorsal/dorsolateral PFC (rPFC, along the right middle/inferior frontal gyrus) approximating Brodmann area nine in attentional performance in humans (Berry et al., 2017; Demeter et al., 2011) that is sensitive to cholinergic manipulation (Berry et al., 2015). Increases in task difficulty (via introduction of a visual distractor) increase rPFC activation and acetylcholine release, which is interpreted to reflect attentional effort in the face of performance decrement. Critically, increases in rPFC measures of effort are predicted by dACC responses to performance decrements (Berry et al., 2017). These findings are consistent with modeling work demonstrating that pairing a conflict signal (ACC signal) with adjustments in the allocation of attention (PFC signal) can accurately simulate trial-based adjustments during attentional challenge (Botvinick et al., 1999, 2001; Logan et al., 1983; Tzelgov et al., 1992).

While increases in effort are reflected in recruitment of rPFC and increased levels of rPFC cholinergic activity (Sarter & Lustig, 2020), recruitment of these systems is often not sufficient to successfully rescue performance. Instead, elevated rPFC cholinergic activity appears to be more predictive of attempts to maintain or recover performance following challenges (Berry et al., 2017; Demeter et al., 2011; Paolone et al., 2012; see also Gritton et al., 2013). These findings join others that have observed activation-demand functions that fit an “inverted U” (Callicott et al., 1999; Reuter-Lorenz & Cappell, 2008; Van Snellenberg et al., 2015). As task difficulty increases, there is an increase in activation to a point, after which there is a drop in activation and performance. As depicted in Figure 5B, inverted U-shaped responses have been reported in mid-dorsal/dorsolateral PFC regions similar to those identified in studies using dSAT (Callicott et al., 1999; Reuter-Lorenz & Cappell, 2008; Van Snellenberg et al., 2015). Additionally, inverted U-shaped responses are reported in posterior parietal and premotor cortices (Callicott et al., 1999; Van Snellenberg et al., 2015), thalamus and striatum (Callicott et al., 1999). Cortical regions typically showing inverted U-shaped responses are displayed in Figure 5B. The convergence of the theoretical prediction and empirical evidence is notable and supports the conceptualization of rPFC as an effort tracking region integrating dACC-midbrain’s motivated demand signals.

Relationship to MIT

The NMAE was developed through empirical research in rodent models and humans but shares important features in common with MIT. For both models, effort scales with perceived task difficulty, which permits difficulty to vary across individuals. Additionally, the patterns of activity of the cholinergic system closely resemble “energization” mechanisms described by Brehm. Brehm conceptualized energization as the “processes by which an organism prepares to undertake an effortful task” (Brehm et al., 1983, p. 22). Empirical studies using the dSAT have demonstrated pretask anticipatory increases in acetylcholine release in rodents. The ramping of cholinergic activity in anticipation of impending cognitive demand is associated with better performance (Paolone et al., 2012; Parikh et al., 2007). Preparatory increases in prefrontal acetylcholine may reflect a neurobiological mechanism of energization and further align patterns of acetylcholine activity with the MIT theoretical framework.

NMAE suggests activation-demand functions fit an “inverted-U,” which is consistent with nonmonotonic responses predicted by MIT where effort is not justified by task importance, and people disengage. Patterns of rodent performance in the dSAT suggest a total loss of motivation following extended elevation of task difficulty, which are so abrupt they resemble a sawtooth rather than inverted-U trajectory. Indeed, task disengagement persists with suppressed performance levels that endure even when task difficulty returns to baseline (Demeter et al., 2008). Additional research in humans is needed to determine whether inverted-U patterns of brain activation reflect loss of motivation, abandoning the current task set to explore alternatives, or some combination of cognitive-motivational processes (Lustig & Sarter, 2015). Testing aging or clinical populations may be critical for establishing to what extent the drop-off point shifts with reductions in neural capacity and is affected by subjective experiences (e.g., Brinkmann & Gendolla, 2007, 2008; Smith & Hess, 2015). Future human studies may resolve these questions by pairing effortful tasks with experience sampling to directly link reductions in task performance with self-reported loss of motivation and disengagement.

General Discussion

The goal of this review was to critically compare influential theories of effort and cognitive control allocation, independently developed to explain psychological, computational, and neurobiological aspects. Specifically, we aimed to contrast the predictions and findings of MIT, a psychological theory proposed decades ago, with those of recent computational and neurobiological models of cognitive control and effort, to determine overlap, divergence, and potential for integration.

Before comparing predictions and mechanisms proposed by these theories, it is crucial to confirm that their main dependent variable is close to the concept of motivational intensity and effort as defined by MIT (Brehm & Self, 1989; Gendolla & Wright, 2009). The EVC theory aims to predict, among others, the amount of cognitive control allocated to a task, which clearly corresponds to the intensity aspect of behavior and the amount of mobilized resources suggested in MIT framework. The RML is concerned, among others, with the optimal allocation of cognitive and physical effort, which therefore perfectly aligns with the explananda of MIT. Finally, NMAE considers effort as the sustained motivated activation of attentional systems, which also corresponds to the idea of resource mobilization and the intensity aspect of behavior. Therefore, altogether, these theories aim to predict a construct that is explicitly or closely associated with the concept of effort as defined in MIT, that is, the mobilization of resources to carry out instrumental behavior (Gendolla & Wright, 2009; see also Massin, 2017).

However, it is of note here that whereas MIT and RML apply to both cognitive and physical effort, previous instantiations of EVC and NMAE primarily focused on cognitive effort (although they can in principle be applied to predict physical effort). Moreover, it appears that these models use different operationalization of effort to test their predictions. MIT predictions were mainly tested using cardiovascular measures of effort during cognitive tasks (see Gendolla & Wright, 2005; Gendolla, Wright, et al., 2012; Richter et al., 2016; Wright & Kirby, 2001, for reviews). In contrast, EVC theory draws on computational simulations to predict the intensity of cognitive control, which may explain various behavioral phenomena in cognitive control tasks, such as the Stroop effect or task performance in cued and voluntary task switching (Lieder et al., 2018; Musslick et al., 2015), as well as the relationship between behavioral and neural correlates of incentive evaluation (using EEG; Frömer et al., 2021) and attentional allocation (using fMRI; Shenhav et al., 2018). The RML framework draws on a more mechanistic account of the neural circuitry underlying effortful behavior to predict both effort-related behavior (decisions and performance) and effort-related neural activity (fMRI-BOLD and EEG activity in humans; single-cell recordings, pharmacological depletion, and lesion studies in animals). Finally, the NMAE draws on fMRI-BOLD (in humans) and measures of cholinergic activity (in animals) to test its predictions. This indicates a striking degree of coherence and interaction among these models, which inform different levels of processes underlying effort allocation. Table 1 provides an overview of the theories and their correspondence regarding effort.

The process of effort allocation is often described as driven by a cost–benefit analysis, weighing potential payoffs against expected costs (e.g., Croxson et al., 2009; Shenhav et al., 2013, 2017). The theories presented in this review suggest slightly different conceptualizations of such costs and benefits, though NMAE does not explicitly address costs of effort allocation, nor the effect of incentives. In MIT and RML, the correspondence is rather straightforward. MIT suggests that the required effort reflects the costs, and success importance, the benefits. When the required effort exceeds success importance (the maximally justified effort), individuals should disengage because the costs exceed the benefits. Similarly, the RML framework considers dACC activity as the results of a cost–benefit trade-off. Hereby, effort is costly as it requires a catecholamine boost. This is traded-off against the reward at stake (i.e., the potential benefits), and the results of this integrative computation determine whether it is worth engaging in the task at hand. This mechanism leads to similar predictions as MIT. Similarly, in EVC theory, benefits are quantified in terms of outcomes associated with allocating cognitive control and the costs are quantified as a function of the amount of control allocated. We previously established a correspondence between

Table 1
Correspondence Between the Theories Regarding Effort

Characteristics	MIT	EVC	RML	NMAE
Conceptual DV	Effort	Cognitive control	Effort allocation	Attentional effort
Determinants	Subjective task difficulty Success importance	Subjective task difficulty Task automaticity Reward Cost of control Control efficacy	Task difficulty (predicted success rate, learned by trial-and-error) Reward (immediate or delayed) Cost of boosting Environmental volatility	Task difficulty (cognitive challenge, performance decrement)
Main neurobiological correlates		dACC	dACC VTA (Dopamine) LC (Noradrenaline)	dACC VTA (Dopamine) Basal Forebrain (Acetylcholine) PFC
Main measure/operationalization	Cardiovascular reactivity	Simulation Behavior fMRI-BOLD activity	Simulation of dACC neural activity (boost) Simulation of behavior fMRI-BOLD activity Behavior	fMRI-BOLD activity in mid-dorsal/dorsolateral PFC

Note. MIT = motivational intensity theory; EVC = expected value of control; RML = reinforcement meta-learner; NMAE = neuronal model of attentional effort; DV = dependent variable; dACC = dorsal anterior cingulate cortex; VTA = ventral tegmental area; LC = locus coeruleus; PFC = prefrontal cortex; fMRI = functional magnetic resonance imaging; BOLD = blood-oxygen-level-dependent.

success importance in MIT and the maximum amount of justified control in EVC theory. Beyond these slight distinctions and various operationalizations of effort, the next section will describe how far the predictions of these models align with those of MIT regarding effort allocation.

Predictions for Fixed and Known Task Difficulty

The first core prediction of MIT is the nonmonotonic relationship between perceived task difficulty and effort (Brehm & Self, 1989; Richter et al., 2016; Wright, 1996). Accordingly, effort is a function of perceived task difficulty as long as success is possible and the required effort is justified by success importance. When the required effort exceeds the level of effort justified by success importance or when the task is perceived as impossible, low effort is predicted (see Figure 1). The expected pattern of effort associated with this prediction is strikingly visible in all discussed models.

As visible in the simulation depicted in Figure 2B, the EVC theory predicts that the amount of control invested increases with expected task difficulty until a maximum tolerable task difficulty is reached and drops sharply if the task becomes more difficult. The maximum worthwhile control intensity (i.e., success importance) determines the maximum tolerable difficulty in a similar fashion as MIT. Thus, MIT and EVC theory make similar predictions about the nonmonotonic relationship between effort investment and task difficulty. According to the RML and as visible in the two simulations depicted in Figure 4, the inverted U-shaped profile of the RML-dACC boosting signal clearly shows that increasing difficulty leads to increase effort allocation up to the point when it is either not worth it or, not possible, when boosting drops. These predictions of the RML are fully in line with those of MIT when considering that the sawtooth pattern of MIT predictions should lead to an inverted-U pattern for a group of individuals (or simulated participants). Finally, the NMAE predicts that effort scales with perceived difficulty until a drop-off point reflecting disengagement. These predictions are reflected in inverted U-shaped responses in effort-related brain areas such as the rPFC, similar to that of RML. Overall, these predictions and findings are in line with the MIT framework.

Altogether, this review indicates that the effort pattern predicted by MIT for fixed and known difficulty is visible in the predictions and supporting simulations or evidence related to the three recent models. It is remarkable to observe that the predictions formulated in MIT decades ago correspond to those of recent models, which indicates that MIT remains a reliable tool to predict effort when task difficulty is fixed and known. This also suggests that MIT predictions apply to various levels of effort mobilization, such as the amount of cognitive control and effort-related brain activity. Finally, this allows establishing connections between the theories presented in this review, developed independently and with scarce attempts at integration so far.

Predictions for Unspecified Task Difficulty

In situations where individuals do not know the difficulty of a task or where they can choose the difficulty of the task, MIT predicts, in line with the resource conservation principle, that individuals will engage effort in proportion to potential motivation, that is, the amount of effort that is justified by success importance. That is, success importance directly determines effort if task difficulty is unspecified, as the allocated amount of effort matches the maximally justified effort. This prediction is clearly similar within the RML framework, which implies that when difficulty is unknown, the amount of effort exerted will solely depend on the reward at stake. The NMAE does not explicitly mention this issue. In contrast, the EVC theory postulates that this is only the case if certain conditions are met, namely if the expected difficulty of a task matches the maximum tolerable difficulty for which an agent would be willing allocate cognitive control. This offers interesting perspectives for future studies to establish how far priors about task difficulty may impact effort even when task difficulty is unspecified. This issue points to the idea that in some cases, task difficulty may not be completely clear and known or completely unspecified but rather anticipated as falling in some intermediate range without knowing exactly where it will fall in that range. In turn, the degree of perceived uncertainty about task difficulty may strongly impact the computation of the effort worth allocating, as suggested in both EVC and RML frameworks. Noteworthy, empirical evidence did show support for a direct impact of success importance on effort when task difficulty is unspecified, as predicted by MIT (e.g., Richter & Gendolla, 2006). In light of EVC theory, these findings suggest that participants expected the task to be difficult enough to justify a maximum allocation of control.

Cognitive and Neurobiological Correlates of Effort

Mounting evidence suggests that the dACC plays a central role in the allocation of effort (Behrens et al., 2007; Botvinick et al., 2001, 2004; Chong et al., 2017; Gehring & Knight, 2000; Holroyd & McClure, 2015; Klein-Flügge et al., 2016; Kolling et al., 2012; Luu et al., 2000; Shenhav et al., 2016; Silvetti et al., 2018; Vassena, Holroyd, et al., 2017), including effort-related cardiovascular reactivity (Critchley et al., 2003; Silvestrini, 2017). However, the underlying mechanisms remain highly debated. This review aimed to go a step further in determining cognitive and neural correlates of effort by comparing the predictions and mechanisms of recent neurocomputational and neuronal models. This comparison revealed a coherent multilevel description of adaptive effort allocation, capturing cognitive, neurobiological, and physiological processes.

Whereas MIT is concerned with the broad motivational determinants of effort, the EVC theory formally describes the decision-making processes underlying the allocation of cognitive control (Shenhav et al., 2013, 2017). In this context, the EVC theory provides explanations regarding the fine-grained cognitive processes beyond the broad constructs of perceived task difficulty and success importance, and their interaction. As presented in Figure 2, this model allows to simulate and precisely predict how much cognitive control an agent will exert depending on the value of performing correctly, the expected probability of succeeding, as well as the costs associated with allocating control to that task. Shenhav and colleagues introduced EVC theory as an integrative perspective of dACC function (based on extensive review of previous work, Shenhav et al., 2013). However, the theory is not constrained to a particular neurobiological implementation of those mechanisms.

Similarly, the RML theory was developed around the key principle that costs and benefits are integrated, and that this computation is carried out by the dACC. RML proposes a neurocomputational mechanisms computing this trade-off (meta-learning), as well as a candidate neurobiological mechanism (dACC—brainstem interaction). This implementation is compatible with the cognitive mechanism proposed by the EVC theory and the psychological mechanism described by MIT. The RML implements dACC as an integrator of predictions with brainstem teaching signals from the VTA (dopamine) and the LC (noradrenaline). Importantly, noradrenergic release implies activation of the sympathetic nervous system, which triggers changes in cardiovascular reactivity. Therefore, RML offers additional support to the view that the dACC integrates information about costs and benefits to determine effort allocation and associated cardiovascular reactivity (Silvestrini, 2017). This allows establishing a strong link between effort allocation processes in the brain and cardiovascular reactivity as measure in the context of MIT. Furthermore, the RML provides the implementation of a neural system that can simulate dACC-VTA-LC interaction, as well as subsequent predicted behavior, allowing simulations of neural lesion or catecholaminergic depletion. This implies the possibility of testing predictions (including those aligned with MIT) in conditions relatable to neurological or psychiatric disorders (Caligiore et al., 2020; Silvetti et al., 2019).

Finally, the NMAE contributes an account of the neural mechanisms underlying the maintenance of attentional effort. In this framework, acetylcholine activity in lateral PFC tracks effort and is stimulated by pathways involving dACC-VTA-basal forebrain-lateral PFC. It is worth noting that this activation/energization of the cholinergic system may also occur through noradrenergic inputs to basal forebrain, offering a point of harmonization of RML and NMAE models. While activation within these lateral PFC regions tracks attentional effort, activation is not systematically associated with increased performance, which is in line with the distinction between effort and performance proposed in the introduction and assumed by MIT framework. In contrast, the maintenance of optimal performance seems rather associated with more posterior parietal sensory areas via cholinergic mechanisms on receptive field properties, synchronized firing, enhancement of thalamic inputs, suppression of associational inputs, and other mechanisms designed to amplify and specify input processing (Sarter et al., 2006). These findings are in line as well with the distinction between control allocation and control implementation as proposed in the EVC framework. Accordingly, the dACC is responsible for determining the amount of control, whereas lateral prefrontal areas are associated with the exertion of control, for instance to maintain task sets (e.g., Kerns et al., 2004; MacDonald et al., 2000; Shenhav et al., 2013, 2017).

Altogether, this review indicates that the discussed models refer to different aspects of effort and actually inform different levels of adaptive resource allocation, including cognitive, neurobiological, and physiological processes, highlighting connections between these different levels. However, these models also have in common the prediction that computation about costs and benefits is implemented within dACC, which determines in turn the amount of resources to allocate. Crucially, these theories propose similar predictions for fixed and known task difficulty and partly similar predictions for unspecified task difficulty. Beyond these common predictions, we summarize in the next section some of the distinctions and strengths of each theory.

Specificity and Strengths of the Theories

One may consider that the greatest strength of MIT is its parsimony (e.g., Epstein, 1984; Nolan, 1997). Drawing on two basic and broad motivational determinants, MIT allows predicting effort as supported by more than a hundred studies (see Gendolla & Wright, 2005; Gendolla, Wright, et al., 2012; Richter et al., 2016; Wright & Kirby, 2001, for reviews), and in line with recent neurocomputational and neuronal models as revealed by the present review (Sarter et al., 2006; Shenhav et al., 2013; Silvetti et al., 2018). Moreover, this theoretical framework allows the integration of any other variable that impacts task difficulty and/or success importance, such as ability beliefs (see Wright, 1998), experienced fatigue (see Wright & Stewart, 2012), mood states (see Gendolla, Wright, et al., 2012), or pain (Cancela & Silvestrini, 2021). This substantially enlarges the scope and applicability of the initial instantiation of MIT. Based on MIT and previous work, it is relatively straightforward to build clear and precise predictions on effort. The graphical representation of the predictions allows determining the amount of effort expected depending on task difficulty and success importance, and their interactions with third variables, such as ability beliefs or mood states. Finally, the numerous evidence based on cardiovascular measures and supporting MIT predictions allowed establishing cardiovascular reactivity as a valid indicator of effort.

The EVC theory builds on a computational approach to derive quantitative and formally rigorous predictions on effort allocation. This model integrates a wide range of empirical findings related to effort allocation by exposing a dissociation between one's *willingness* to exert cognitive control, as determined by motivational factors (e.g., a person's sensitivity to reward or expectations about task difficulty), and one's capacity for cognitive control, as determined by intrinsic limitations (Lieder et al., 2018; Musslick, Cohen, et al., 2018; Musslick et al., 2015, 2019). For example, the model can offer novel perspectives on how positive or negative affect influences one's motivation to exert cognitive effort (Grahek et al., 2020), suggesting that affect can alter the perception of rewarding outcomes. It has also influenced the understanding of cognitive impairments in psychiatric disorders, adding the possibility that deficits in task performance stem from changes in the decision-making process about effort allocation (Grahek et al., 2019). Finally, as demonstrated above, the EVC theory can be leveraged to quantify the relationship between the different variables considered in MIT. For instance, whereas MIT considers perceived difficulty as a broad concept, EVC offers more precise prediction about the impact of the characteristics of the task versus performance standards. Overall, the EVC theory provides fine-grained computational mechanisms underlying motivated cognitive control as well as potential dysfunctions of cognitive control.

The RML theory builds on a quantitative and formally rigorous computational approach as well. While both EVC and RML theory are conceived as theories of dACC function, RML is designed to explain adaptive behaviors relying on the interaction between dACC-brainstem circuits, offering a more mechanistic account of associated neural dynamics and explaining learning dynamics beyond effort allocation. Its broader explanatory scope includes other effects observed in this network (e.g., volatility and control of learning rate, higher order conditioning). Concerning effort allocation, RML highlights critical role of recursive loops between the dACC and the brainstem, explaining the contribution of dopamine and noradrenaline release (known to be central in the context of reward processing and energization of behavior, respectively). Furthermore, it captures the mechanism by which effort allocation is implemented in terms of energization of behavior, via noradrenaline release toward task-relevant areas. Known to have an impact on pupil dilation, such increase may well correlate with cardiovascular measures known to track effort investment according to MIT. Finally, the RML theory builds on a central tenet that effort allocation derives from adaptive learning and provides a computational characterization thereof. This offers perspectives on how individuals shape their effort-related decision processes according to their experience and on interindividual differences in effort allocation, with critical implications for treatment of clinical disorders with motivational impairments. The simulated neural machinery allows making neural and behavioral predictions of consequences of catecholaminergic alterations, a promising tool for estimating underlying neuromodulatory deficits in neuropsychiatric disorder without invasive measurements.

The NMAE highlights the role of prefrontal cholinergic activity in effortful processes. Moreover, it provides a clear dissociation between regions associated with attentional effort and performance. Especially, it offers insight into the neural processes associated with the allocation of effort and the execution of action through increased efficiency in sensory areas. Finally, the theory applies to a large spectrum from rodent models to psychopathology.

All of the presented theories are challenged by effort allocation patterns violating the predicted inverted-U pattern of effort investment as a function of perceived task difficulty and subjective value. The empirical finding of a monotonic relationship or regular U-shaped pattern between effort and task difficulty, ranging from easy levels of difficulty to levels at which the task becomes impossible to perform, would be considered counterevidence to prior instantiations of all presented models. Furthermore, MIT, EVC, and RML theories suggest that when task difficulty is unspecified an increase in the subjective value of a task should lead to (a) a higher likelihood of choosing to perform this task (EVC and RML) and (b) a higher amount of effort allocated to the task (MIT, EVC, and RML). This predicted monotonicity of the relationship between subjective value and effort has been treated more formally in economic theories of rational inattention (e.g., Caplin et al., 2020; Caplin & Dean, 2015) and provides the basis for the reliable estimation of effort costs from human performance (Caplin et al., 2020; Musslick, Cohen, et al., 2018). Evidence that participants showed less effort allocation in response to greater rewards, all else being equal, would appeal to further mechanisms. Aberrances from optimal behavior, as predicted by these theories, may also further our understanding of disorders with motivational impairments (Grahek et al., 2019).

Notable Conceptual Differences Between Recent Theories

While the primary purpose of this article is to integrate recent neurocomputational models of effort allocation with MIT, it is worth highlighting differences between the three models that we contrasted with MIT. The first difference pertains to the translation of effort into performance. All models assume a gradual variation of the effort signal, whether it be in terms of control signal intensity (EVC), boosting (RML), or attentional effort signal (NMAE). Furthermore, all models assume a continuous effect of those signals on task performance. However, in contrast to NMAE, both RML and EVC have been used to implement the impact of effort allocation on behavior: both implement behavior in that they translate their signals into a decision (e.g., engage, do not engage, choose Option A) or into the selection of the correct result in a performance task. Instances of EVC theory simulate both action selection (e.g., task choice) and task performance (e.g., reaction time), by first computing the optimal effort signals (based on a control allocation module) and then linking these signals to the parameters of a process module (e.g., the drift diffusion model; Ratcliff, 1978). To compute the optimal control signal, the control allocation module may rely on knowledge about the environment, as well as internal representations of how control signals translate into performance. RML performs similar computations to EVC and can be connected to an external process module (e.g., a drift diffusion model). In contrast, RML also has an in-built action selection module. Thus, RML simulates behavior (and the effect of effort on it) via the boosting signal. However, unlike the control signal in EVC, the boosting signal modulates both action selection and motivation (the reward signal) to find the optimal policy.

Another difference between the RML and EVC models pertains to the computation of costs associated with effort exertion. Both models assume that the cost of effort scales with the amount of effort exerted. However, EVC and RML approach the stability–flexibility trade-off in selecting the optimal control signal in a different way. Instances of EVC theory have assumed that the effort cost scales with the change in the effort signal, resulting in a task reconfiguration cost (Musslick et al., 2015). In contrast, within RML, effort cost is purely a function of boosting (irrespective of whether the selected boosting level is the same or different from the previous trial). This leads to model-specific predictions: EVC assumes that a change in control signal is generally associated with a cost, promoting stability over implemented control signals; conversely, RML reacts to task volatility, with changing boosting signal being less likely during stationary periods and more likely during volatile periods (due to the adaptive learning rate).

Moreover, in both RML and EVC models, a greater effort signal allocated to the relevant task will generally result in better performance. Despite these similarities between EVC and RML in contrast to NMAE, all three models differ in terms of what is being learned from experience. EVC theory, as originally stated in Shenhav et al. (2013), suggests that the system may learn components (e.g., expectations of task difficulty or prospective rewards) that factor into the computation of the EVC. These learning processes may factor into trial-by-trial changes in control allocation and concomitant adjustments in behavior (Musslick et al., 2015, 2019; Bustamante et al., 2021). An extension of the EVC model proposes a mechanism for learning the value of effort directly from reinforcement, using Bayesian linear regression (Lieder et al., 2018; Bustamante et al., 2021). RML also learns the value of allocating effort directly from reinforcement (i.e., when receiving a reward following successful performance, Silvetti et al., 2018) and adaptively adjusts its (internal and behavioral) parameters in a trial-by-trial fashion. However, unlike the model proposed by Lieder et al. (2018), RML also implements the optimization of learning rates (leveraging Bayesian optimization), so to perform well in volatile environments (with changing reward contingencies). As a consequence, RML tracks well task volatility, adapting effort exertion dynamically. In contrast, while it is plausible to assume that factors determining attentional adjustment in NMAE (e.g., the expectation of a cognitive challenge) may be learned from experience as well, no implementation for such dynamics is proposed by NMAE.

Both EVC and RML differentiate themselves further from NMAE in that they provide a computational characterization of the relationship between expected reward and effort. That is, NMAE focuses on the neural mechanisms underlying effort mobilization under the assumption that participants see value in performing the task, without considering the influence of extrinsic rewards. RML further proposes that the boosting signal modulates not only effort exerted but also motivation in terms of reward signal (and related dopaminergic output). In relation to this, EVC theory focuses on explaining the computational and behavioral mechanisms of control allocation without constraining itself to a specific neural implementation. RML is built as a neurobiologically plausible computational agent, thus proposing a computational mechanism and an underlying neural implementation at the circuit level (although not constrained to it). NMAE proposes a neural implementation, without a specific computational implementation.

These differences between the three theories derive, in part, from their explanatory scope. EVC theory considered a general framework that has focused on explaining behavioral phenomena at the intersection of motivation and cognitive control, as well as on providing an integrative account of dACC function in terms of expected value computation. In contrast, NMAE was designed as a model of the neural machinery underlying attentional effort specifically (without references to value computation). RML was conceived as a general mechanistic quantitative model of adaptive reinforcement learning and motivation (beyond effort allocation alone), with a key role for meta-learning in reward-contingency coding, volatility tracking, and effortful action.

Open Questions and Future Perspectives

It remains an open question whether the relationship between subjective task difficulty and effort, at least until the drop-off point, is strictly linear as suggested by MIT. In the EVC theory, the ascend appears to be almost linear but is plausibly not exactly linear and slightly concave. This may depend on the assumptions about the cost function (exponential vs. linear), as well as the performance metric being optimized as a function of control (e.g., accuracy vs. reward rate). The RML theory and the NMAE rather suggest an inverted U shape, which corresponds to the idea that individuals should vary in terms of perceived difficulty and drop-off point, as presented in the introduction. Here, the principle of parsimony may lead to the conclusion that the linear trend represents the simplest and most efficient way to describe this relationship at the individual level, whereas, in practical, averaged data of individuals rather reveal a curvilinear pattern.

Interestingly, several lines of research show that the dACC (or the closely related anterior mid-cingulate cortex [aMCC]) is associated not only with effort and cognitive control but also with phenomena such as negative affect and pain (e.g., Rainville et al., 1997; Shackman et al., 2011; Wager et al., 2016). This potentially reveals control processes that are common to these domains (Shackman et al., 2011) and it remains an open question how the neurocognitive models presented in this review may inform such processes. In this context, recent work drawing on multivariate pattern analyses suggests that local patterns within the aMCC may distinguish between various domains such as cognitive control and pain (Kragel et al., 2018; Silvestrini et al., 2020; Vermeylen et al., 2020). These findings open new perspectives in the study of dACC functional specificity and mechanisms in different domains beyond common fMRI activity at the gross anatomical level. In this context, it is important to keep in mind that the present review is not exhaustive and that other models ascribe different functions to the dACC (Alexander & Brown, 2011; Holroyd & McClure, 2015; Kolling et al., 2012). Future reviews may enlarge the comparison to these models to help establishing a comprehensive understanding of the role or roles of dACC and other regions in effortful processes.

An interesting open empirical question concerns the phenomenology of effort (Inzlicht et al., 2018; Saunders et al., 2015). The source of the subjective experience of effort remains highly debated (Kurzban et al., 2013). Based on RML's functional architecture, one could test whether subjective perception of effort is tracked by the RML-dACC boosting signal (potentially in synergy with other brain regions often coactive with dACC during effort discounting and exertion and known to contribute to interoception such as the anterior insular cortex; Arulpragasam et al., 2018; Chong et al., 2017).

Finally, one may take advantage of this review to complement and inform the theories. For instance, it appears that the explanation of the drop-off point in the context of the NMAE remains speculative. Building on MIT and on the predicted interaction between subjective task difficulty and success importance, future studies drawing on the NMAE may investigate more precisely the determinants of this drop-off point in healthy or clinical population.

Conclusion

This review aimed to compare several theories related to effort. Most important, it appears that the predictions of MIT regarding fixed and known difficulty are shared with the three other theories and associated supporting evidence. In contrast, the predictions for unspecified task difficulty are similar in MIT and RML, and partly similar in EVC. Interestingly, whereas these theories propose relatively comparable predictions regarding effort allocation, they concern different operationalizations of effort, as well as different levels of analysis. This allows describing an overall view of effort mechanisms related to cognitive computation, neurobiological mechanisms, macro psychological determinants, physiological reactivity, and their plausible interconnections. We hope that this review may help further establishing a firm and comprehensive knowledge about effort.

References

Alexander, W. H., & Brown, J. W. (2011). Medial prefrontal cortex as an action-outcome predictor. *Nature Neuroscience*, *14*(10), 1338–1344. https://doi.org/10.1038/nn.2921

Arulpragasam, A. R., Cooper, J. A., Nuutinen, M. R., & Treadway, M. T. (2018). Corticoinsular circuits encode subjective value expectation and violation for effortful goal-directed behavior. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(22), E5233–E5242. https://doi.org/10.1073/pnas.1800444115

Behrens, T. E. J., Woolrich, M. W., Walton, M. E., & Rushworth, M. F. S. (2007). Learning the value of information in an uncertain world. *Nature Neuroscience*, *10*(9), 1214–1221. https://doi.org/10.1038/nn1954

Berry, A. S., Blakely, R. D., Sarter, M., & Lustig, C. (2015). Cholinergic capacity mediates prefrontal engagement during challenges to attention: Evidence from imaging genetics. *NeuroImage*, *108*, 386–395. https://doi.org/10.1016/j.neuroimage.2014.12.036

Berry, A. S., Sarter, M., & Lustig, C. (2017). Distinct frontoparietal networks underlying attentional effort and cognitive control. *Journal of Cognitive Neuroscience*, *29*(7), 1212–1225. https://doi.org/10.1162/jocn_a_01112

Bijleveld, E., Custers, R., & Aarts, H. (2009). The unconscious eye opener: Pupil dilation reveals strategic recruitment of resources upon presentation of subliminal reward cues. *Psychological Science*, *20*(11), 1313–1315. https://doi.org/10.1111/j.1467-9280.2009.02443.x

Boksem, M. A. S., Meijman, T. F., & Lorist, M. M. (2005). Effects of mental fatigue on attention: An ERP study. *Cognitive Brain Research*, *25*(1), 107–116. https://doi.org/10.1016/j.cogbrainres.2005.04.011

Botvinick, M., & Braver, T. (2015). Motivation and cognitive control: From behavior to neural mechanism. *Annual Review of Psychology*, *66*(1), 83–113. https://doi.org/10.1146/annurev-psych-010814-015044

Botvinick, M., Nystrom, L. E., Fissell, K., Carter, C. S., & Cohen, J. D. (1999). Conflict monitoring versus selection-for-action in anterior cingulate cortex. *Nature*, *402*(6758), 179–181. https://doi.org/10.1038/46035

Botvinick, M. M., Braver, T. S., Barch, D. M., Carter, C. S., & Cohen, J. D. (2001). Conflict monitoring and cognitive control. *Psychological Review*, *108*(3), 624–652. https://doi.org/10.1037/0033-295X.108.3.624

Botvinick, M. M., Cohen, J. D., & Carter, C. S. (2004). Conflict monitoring and anterior cingulate cortex: An update. *Trends in Cognitive Sciences*, *8*(12), 539–546. https://doi.org/10.1016/j.tics.2004.10.003

Brehm, J. W. (1975). *Research on motivational suppression* [Research Proposal submitted to the National Science Foundation]. Department of Psychology, University of Kansas.

Brehm, J. W., & Self, E. A. (1989). The intensity of motivation. *Annual Review of Psychology*, *40*(1), 109–131. https://doi.org/10.1146/annurev.ps.40.020189.000545

Brehm, J. W., Wright, R. A., Solomon, S., Silka, L., & Greenberg, J. (1983). Perceived difficulty, energization, and the magnitude of goal valence. *Journal of Experimental Social Psychology*, *19*(1), 21–48. https://doi.org/10.1016/0022-1031(83)90003-3

Brickenkamp, R., & Zillmer, E. (1998). *D2 test of attention*. Hogrefe & Huber.

Brinkmann, K., & Gendolla, G. H. E. (2007). Dysphoria and mobilization of mental effort: Effects on cardiovascular reactivity. *Motivation and Emotion*, *31*(1), 71–82. https://doi.org/10.1007/s11031-007-9054-0

Brinkmann, K., & Gendolla, G. H. E. (2008). Does depression interfere with effort mobilization? Effects of dysphoria and task difficulty on cardiovascular response. *Journal of Personality and Social Psychology*, *94*(1), 146–157. https://doi.org/10.1037/0022-3514.94.1.146

Bustamante, L., Lieder, F., Musslick, S., Shenhav, A., & Cohen, J. (2021). Learning to overexert cognitive control in a Stroop task. *Cognitive, Affective, & Behavioral Neuroscience*, *21*(3), 453–471. https://doi.org/10.3758/s13415-020-00845-x

Caligiore, D., Silvetti, M., D'Amelio, M., Puglisi-Allegra, S., & Baldassarre, G. (2020). Computational modeling of catecholamines dysfunction in Alzheimer's disease at pre-plaque stage. *Journal of Alzheimer's Disease*, *77*(1), 275–290. https://doi.org/10.3233/JAD-200276

Callicott, J. H., Mattay, V. S., Bertolino, A., Finn, K., Coppola, R., Frank, J. A., Goldberg, T. E., & Weinberger, D. R. (1999). Physiological characteristics of capacity constraints in working memory as revealed by functional MRI. *Cerebral Cortex*, *9*(1), 20–26. https://doi.org/10.1093/cercor/9.1.20

Cancela, T., & Silvestrini, N. (2021). Impact of pain on mental effort assessed as cardiovascular reactivity. *Pain Reports*, *6*(1), Article e917. https://doi.org/10.1097/PR9.0000000000000917

Caplin, A., Csaba, D., Leahy, J., & Nov, O. (2020). Rational inattention, competitive supply, and psychometrics. *The Quarterly Journal of Economics*, *135*(3), 1681–1724. https://doi.org/10.1093/qje/qjaa011

Caplin, A., & Dean, M. (2015). Revealed preference, rational inattention, and costly information acquisition. *The American Economic Review*, *105*(7), 2183–2203. https://doi.org/10.1257/aer.20140117

Chong, T. T.-J., Apps, M., Giehl, K., Sillence, A., Grima, L. L., & Husain, M. (2017). Neurocomputational mechanisms underlying subjective valuation of effort costs. *PLoS Biology*, *15*(2), Article e1002598. https://doi.org/10.1371/journal.pbio.1002598

Cohen, J. D., Dunbar, K., & McClelland, J. L. (1990). On the control of automatic processes: A parallel distributed processing account of the Stroop effect. *Psychological Review*, *97*(3), 332–361. https://doi.org/10.1037/0033-295X.97.3.332

Cools, R. (2019). Chemistry of the adaptive mind: Lessons from dopamine. *Neuron*, *104*(1), 113–131. https://doi.org/10.1016/j.neuron.2019.09.035

Critchley, H. D., Mathias, C. J., Josephs, O., O'Doherty, J., Zanini, S., Dewar, B.-K., Cipolotti, L., Shallice, T., & Dolan, R. J. (2003). Human cingulate cortex and autonomic control: Converging neuroimaging and clinical evidence. *Brain: A Journal of Neurology*, *126*(Pt. 10), 2139–2152. https://doi.org/10.1093/brain/awg216

Croxson, P. L., Walton, M. E., O'Reilly, J. X., Behrens, T. E. J., & Rushworth, M. F. S. (2009). Effort-based cost-benefit valuation and the human brain. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *29*(14), 4531–4541. https://doi.org/10.1523/JNEUROSCI.4515-08.2009

da Silva Castanheira, K., LoParco, S., & Otto, A. R. (2021). Task-evoked pupillary responses track effort exertion: Evidence from task-switching. *Cognitive, Affective, & Behavioral Neuroscience*, *21*, 592–606. https://doi.org/10.3758/s13415-020-00843-z

Deco, G., & Thiele, A. (2009). Attention: Oscillations and neuropharmacology. *European Journal of Neuroscience*, *30*(3), 347–354. https://doi.org/10.1111/j.1460-9568.2009.06833.x

Demeter, E., Hernandez-Garcia, L., Sarter, M., & Lustig, C. (2011). Challenges to attention: A continuous arterial spin labeling (ASL) study of the effects of distraction on sustained attention. *NeuroImage*, *54*(2), 1518–1529. https://doi.org/10.1016/j.neuroimage.2010.09.026

Demeter, E., & Sarter, M. (2013). Leveraging the cortical cholinergic system to enhance attention. *Neuropharmacology*, *64*, 294–304. https://doi.org/10.1016/j.neuropharm.2012.06.060

Demeter, E., Sarter, M., & Lustig, C. (2008). Rats and humans paying attention: Cross-species task development for translational research. *Neuropsychology*, *22*(6), 787–799. https://doi.org/10.1037/a0013712

Epstein, R. (1984). The principle of parsimony and some applications in psychology. *Journal of Mind and Behavior*, *5*(2), 119–130. http://www.jstor.org/stable/43853318

Festinger, L. (1957). *A theory of cognitive dissonance*. Stanford University Press.

Frömer, R., Lin, H., Dean Wolf, C. K., Inzlicht, M., & Shenhav, A. (2021). Expectations of reward and efficacy guide cognitive control allocation. *Nature Communications*, *12*(1), Article 1030. https://doi.org/10.1038/s41467-021-21315-z

Geen, R. G. (1995). *Human motivation: A social psychological approach*. Thomson Brooks/Cole Publishing.

Gehring, W. J., & Knight, R. T. (2000). Prefrontal-cingulate interactions in action monitoring. *Nature Neuroscience*, *3*(5), 516–520. https://doi.org/10.1038/74899

Gendolla, G. H. E. (2012). Implicit affect primes effort: A theory and research on cardiovascular response. *International Journal of Psychophysiology*, *86*(2), 123–135. https://doi.org/10.1016/j.ijpsycho.2012.05.003

Gendolla, G. H. E., Brinkmann, K., & Silvestrini, N. (2012). Gloomy and lazy? On the impact of mood and depressive symptoms on effort-related cardiovascular response. In R. A. Wright & G. H. E. Gendolla (Eds.), *How motivation affects cardiovascular response: Mechanisms and applications* (pp. 139–155). American Psychological Association. https://doi.org/10.1037/13090-007

Gendolla, G. H. E., & Richter, M. (2004). The role of mood states in the development of cardiovascular disease: Implications of a motivational analysis of cardiovascular reactivity in active coping. In F. Colombus (Ed.), *Advances in psychology research* (Vol. 33, pp. 139–157). Nova Science Publishers.

Gendolla, G. H. E., & Richter, M. (2006). Cardiovascular reactivity during performance under social observation: The moderating role of task difficulty. *International Journal of Psychophysiology*, *62*(1), 185–192. https://doi.org/10.1016/j.ijpsycho.2006.04.002

Gendolla, G. H. E., & Richter, M. (2010). Effort mobilization when the self is involved: Some lessons from the cardiovascular system. *Review of General Psychology*, *14*(3), 212–226. https://doi.org/10.1037/a0019742

Gendolla, G. H. E., & Silvestrini, N. (2011). Smiles make it easier and so do frowns: Masked affective stimuli influence mental effort. *Emotion*, *11*(2), 320–328. https://doi.org/10.1037/a0022593

Gendolla, G. H. E., & Wright, R. A. (2005). Motivation in social settings: Studies of effort-related cardiovascular arousal. In J. P. Forgas, K. Williams, & W. von Hippel (Eds.), *Social motivation* (pp. 71–90). Cambridge University Press.

Gendolla, G. H. E., & Wright, R. A. (2009). Effort. In D. Sander & K. R. Scherer (Eds.), *The Oxford companion to emotion and the affective science* (pp. 134–135). Oxford University Press.

Gendolla, G. H. E., Wright, R. A., & Richter, M. (2012). Effort intensity: Some insights from the cardiovascular system. In R. M. Ryan (Ed.), *The Oxford handbook of human motivation* (pp. 420–438). Oxford University Press, Scopus.

Gibson, W. R. B. (1900). The principle of least action as a psychological principle. *Mind*, *9*(36), 469–495. https://doi.org/10.1093/mind/IX.36.469

Gilzenrat, M. S., Nieuwenhuis, S., Jepma, M., & Cohen, J. D. (2010). Pupil diameter tracks changes in control state predicted by the adaptive gain theory of locus coeruleus function. *Cognitive, Affective & Behavioral Neuroscience*, *10*(2), 252–269. https://doi.org/10.3758/CABN.10.2.252

Giocomo, L. M., & Hasselmo, M. E. (2007). Neuromodulation by glutamate and acetylcholine can change circuit dynamics by regulating the relative influence of afferent input and excitatory feedback. *Molecular Neurobiology*, *36*(2), 184–200. https://doi.org/10.1007/s12035-007-0032-z

Grahek, I., Musslick, S., & Shenhav, A. (2020). A computational perspective on the roles of affect in cognitive control. *International Journal of Psychophysiology*, *151*, 25–34. https://doi.org/10.1016/j.ijpsycho.2020.02.001

Grahek, I., Shenhav, A., Musslick, S., Krebs, R. M., & Koster, E. H. W. (2019). Motivation and cognitive control in depression. *Neuroscience and Biobehavioral Reviews*, *102*, 371–381. https://doi.org/10.1016/j.neubiorev.2019.04.011

Granholm, E. L., Panizzon, M. S., Elman, J. A., Jak, A. J., Hauger, R. L., Bondi, M. W., Lyonsm M. J., Franz, C. E., & Kremen, W. S. (2017). Pupillary responses as a biomarker of early risk for Alzheimer's disease. *Journal of Alzheimer's Disease*, *56*(4), 1419–1428. https://doi.org/10.3233/JAD-161078

Gritton, H. J., Stasiak, A. M., Sarter, M., & Lee, T. M. (2013). Cognitive performance as a zeitgeber: Cognitive oscillators and cholinergic modulation of the SCN entrain circadian rhythms. *PLOS ONE*, *8*(2), Article e56206. https://doi.org/10.1371/journal.pone.0056206

Hasselmo, M. E., & Sarter, M. (2011). Modes and models of forebrain cholinergic neuromodulation of cognition. *Neuropsychopharmacology*, *36*(1), 52–73. https://doi.org/10.1038/npp.2010.104

Heishman, S. J., Taylor, R. C., & Henningfield, J. E. (1994). Nicotine and smoking: A review of effects on human performance. *Experimental and Clinical Psychopharmacology*, *2*(4), 345–395. https://doi.org/10.1037/1064-1297.2.4.345

Hockey, G. R. J. (1997). Compensatory control in the regulation of human performance under stress and high workload; a cognitive-energetical framework. *Biological Psychology*, *45*(1–3), 73–93. https://doi.org/10.1016/S0301-0511(96)05223-4

Holroyd, C. B. (2016). The waste disposal problem of effortful control. In T. S. Braver (Ed.), *Frontiers of cognitive psychology. Motivation and cognitive control* (pp. 235–260). Routledge/Taylor & Francis.

Holroyd, C. B., & McClure, S. M. (2015). Hierarchical control over effortful behavior by rodent medial frontal cortex: A computational model. *Psychological Review*, *122*(1), 54–83. https://doi.org/10.1037/a0038339

Holroyd, C. B., Nieuwenhuis, S., Yeung, N., Nystrom, L., Mars, R. B., Coles, M. G. H., & Cohen, J. D. (2004). Dorsal anterior cingulate cortex shows fMRI response to internal and external error signals. *Nature Neuroscience*, *7*(5), 497–498. https://doi.org/10.1038/nn1238

Hull, C. L. (1943). *Principles of behavior*. Appleton-Century.

Husain, M., & Roiser, J. P. (2018). Neuroscience of apathy and anhedonia: A transdiagnostic approach. *Nature Reviews Neuroscience*, *19*(8), 470–484. https://doi.org/10.1038/s41583-018-0029-9

Iannaccone, R., Hauser, T. U., Staempfli, P., Walitza, S., Brandeis, D., & Brem, S. (2015). Conflict monitoring and error processing: New insights from simultaneous EEG-fMRI. *NeuroImage*, *105*, 395–407. https://doi.org/10.1016/j.neuroimage.2014.10.028

Inzlicht, M., Shenhav, A., & Olivola, C. Y. (2018). The effort paradox: Effort is both costly and valued. *Trends in Cognitive Sciences*, *22*, 337–349. https://doi.org/10.1016/j.tics.2018.01.007

Jessup, R. K., Busemeyer, J. R., & Brown, J. W. (2010). Error effects in anterior cingulate cortex reverse when error likelihood is high. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *30*(9), 3467–3472. https://doi.org/10.1523/JNEUROSCI.4130-09.2010

Joshi, S., Li, Y., Kalwani, R. M., & Gold, J. I. (2016). Relationships between pupil diameter and neuronal activity in the locus coeruleus, colliculi, and cingulate cortex. *Neuron*, *89*(1), 221–234. https://doi.org/10.1016/j.neuron.2015.11.028

Jurado, M. B., & Rosselli, M. (2007). The elusive nature of executive functions: A review of our current understanding. *Neuropsychology Review*, *17*(3), 213–233. https://doi.org/10.1007/s11065-007-9040-z

Kahneman, D. (1973). *Attention and effort*. Prentice-Hall.

Kahneman, D., & Beatty, J. (1966). Pupil diameter and load on memory. *Science*, *154*(3756), 1583–1585. https://doi.org/10.1126/science.154.3756.1583

Kerns, J. G., Cohen, J. D., MacDonald, A. W., III, Cho, R. Y., Stenger, V. A., & Carter, C. S. (2004). Anterior cingulate conflict monitoring and adjustments in control. *Science*, *303*(5660), 1023–1026. https://doi.org/10.1126/science.1089910

Klein-Flügge, M. C., Kennerley, S. W., Friston, K., & Bestmann, S. (2016). Neural signatures of value comparison in human cingulate cortex during decisions requiring an effort-reward trade-off. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *36*(39), 10002–10015. https://doi.org/10.1523/JNEUROSCI.0292-16.2016

Kolling, N., Behrens, T. E. J., Mars, R. B., & Rushworth, M. F. S. (2012). Neural mechanisms of foraging. *Science*, *336*(6077), 95–98. https://doi.org/10.1126/science.1216930

Kool, W., McGuire, J. T., Rosen, Z. B., & Botvinick, M. M. (2010). Decision making and the avoidance of cognitive demand. *Journal of Experimental Psychology: General*, *139*(4), 665–682. https://doi.org/10.1037/a0020198

Kool, W., Shenhav, A., & Botvinick, M. M. (2017). Cognitive control as cost-benefit decision making. In T. Egner (Ed.), *The Wiley handbook of cognitive control* (pp. 167–189). Wiley Blackwell. https://doi.org/10.1002/9781118920497.ch10

Kop, W. J. (1999). Chronic and acute psychological risk factors for clinical manifestations of coronary artery disease. *Psychosomatic Medicine*, *61*(4), 476–487. https://doi.org/10.1097/00006842-199907000-00012

Kragel, P. A., Kano, M., Van Oudenhove, L., Ly, H. G., Dupont, P., Rubio, A., Delon-Martin, C., Bonaz, B. L., Manuck, S. B., Gianaros, P. J., Ceko, M., Reynolds Losin, E. A., Woo, C. W., Nichols, T. E., & Wager, T. D. (2018). Generalizable representations of pain, cognitive control, and negative emotion in medial frontal cortex. *Nature Neuroscience*, *21*(2), 283–289. https://doi.org/10.1038/s41593-017-0051-7

Kukla, A. (1972). Foundations of an attributional theory of performance. *Psychological Review*, *79*(6), 454–470. https://doi.org/10.1037/h0033494

Kurzban, R., Duckworth, A., Kable, J. W., & Myers, J. (2013). An opportunity cost model of subjective effort and task performance. *Behavioral and Brain Sciences*, *36*(6), 661–679. https://doi.org/10.1017/S0140525X12003196

Lieder, F., Shenhav, A., Musslick, S., & Griffiths, T. L. (2018). Rational metareasoning and the plasticity of cognitive control. *PLoS Computational Biology*, *14*(4), Article e1006043. https://doi.org/10.1371/journal.pcbi.1006043

Linden, D. E. J., Bittner, R. A., Muckli, L., Waltz, J. A., Kriegeskorte, N., Goebel, R., Singer, W., & Munk, M. H. J. (2003). Cortical capacity constraints for visual working memory: Dissociation of fMRI load effects in a fronto-parietal network. *NeuroImage*, *20*(3), 1518–1530. https://doi.org/10.1016/j.neuroimage.2003.07.021

Locke, E. A., & Latham, G. P. (1990). *A theory of goal setting and task performance*. Prentice-Hall.

Locke, E. A., & Latham, G. P. (2019). The development of goal setting theory: A half century retrospective. *Motivation Science*, *5*, 93–105. https://doi.org/10.1037/mot0000127

Logan, G. D., Zbrodoff, N. J., & Fostey, A. R. W. (1983). Costs and benefits of strategy construction in a speeded discrimination task. *Memory & Cognition*, *11*(5), 485–493. https://doi.org/10.3758/BF03196985

Lustig, C., & Sarter, M. (2015). Attention and the cholinergic system: Relevance to schizophrenia. In T. W. Robbins & B. J. Sahakian (Eds.), *Translational neuropsychopharmacology* (Vol. 28, pp. 327–362). Springer International Publishing. https://doi.org/10.1007/7854_2015_5009

Luu, P., Flaisch, T., & Tucker, D. M. (2000). Medial frontal cortex in action monitoring. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *20*(1), 464–469. https://doi.org/10.1523/JNEUROSCI.20-01-00464.2000

MacDonald, A. W., III, Cohen, J. D., Stenger, V. A., & Carter, C. S. (2000). Dissociating the role of the dorsolateral prefrontal and anterior cingulate cortex in cognitive control. *Science*, *288*(5472), 1835–1838. https://doi.org/10.1126/science.288.5472.1835

Manohar, S. G., Chong, T. T.-J., Apps, M. A. J., Batla, A., Stamelou, M., Jarman, P. R., Bhatia, K. P., & Husain, M. (2015). Reward pays the cost of noise reduction in motor and cognitive control. *Current Biology*, *25*(13), 1707–1716. https://doi.org/10.1016/j.cub.2015.05.038

Mante, V., Sussillo, D., Shenoy, K. V., & Newsome, W. T. (2013). Context-dependent computation by recurrent dynamics in prefrontal cortex. *Nature*, *503*(7474), 78–84. https://doi.org/10.1038/nature12742

Massin, O. (2017). Towards a definition of efforts. *Motivation Science*, *3*(3), 230–259. https://doi.org/10.1037/mot0000066

Mather, M., Clewett, D., Sakaki, M., & Harley, C. W. (2016). Norepinephrine ignites local hotspots of neuronal excitation: How arousal amplifies selectivity in perception and memory. *Behavioral and Brain Sciences*, *39*, Article e200. https://doi.org/10.1017/S0140525X15000667

McGaughy, J., Kaiser, T., & Sarter, M. (1996). Behavioral vigilance following infusions of 192 IgG-saporin into the basal forebrain: Selectivity of the behavioral impairment and relation to cortical AChE-positive fiber density. *Behavioral Neuroscience*, *110*(2), 247–265. https://doi.org/10.1037/0735-7044.110.2.247

Miller, E. K., & Cohen, J. D. (2001). An integrative theory of prefrontal cortex function. *Annual Review of Neuroscience*, *24*(1), 167–202. https://doi.org/10.1146/annurev.neuro.24.1.167

Miller, E. K., & Wallis, J. D. (2009). Executive function and higher-order cognition: Definition and neural substrates. In L. R. Squire (Ed.), *Encyclopedia of neuroscience* (Vol. 4, pp. 99–104). Academic Press. https://doi.org/10.1016/B978-008045046-9.00418-6

Miyake, A., Friedman, N. P., Emerson, M. J., Witzki, A. H., Howerter, A., & Wager, T. D. (2000). The unity and diversity of executive functions and their contributions to complex "Frontal Lobe" tasks: A latent variable analysis. *Cognitive Psychology*, *41*(1), 49–100. https://doi.org/10.1006/cogp.1999.0734

Muir, J. L., Everitt, B. J., & Robbins, T. W. (1994). AMPA-induced excitotoxic lesions of the basal forebrain: A significant role for the cortical cholinergic system in attentional function. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *14*(4), 2313–2326. https://doi.org/10.1523/JNEUROSCI.14-04-02313.1994

Musslick, S., Botvinick, M. M., Shenhav, A., & Cohen, J. D. (2015). *A computational model of control allocation based on the Expected Value of Control* [Conference session]. Reinforcement Learning and Decision Making Conference. Edmonton, Alberta, CA.

Musslick, S., & Cohen, J. D. (2021). Rationalizing constraints on the capacity for cognitive control. *Trends in Cognitive Sciences*, *25*(9), 757–775. https://doi.org/10.1016/j.tics.2021.06.001

Musslick, S., Cohen, J. D., & Shenhav, A. (2018). Estimating the costs of cognitive control from task performance: Theoretical validation and potential pitfalls. In T. T. Rogers, M. Rau, X. Zhu, & C. W. Kalish (Eds.), *Proceedings of the 40th annual conference of the Cognitive Science Society* (pp. 798–803). Cognitive Science Society.

Musslick, S., Cohen, J. D., & Shenhav, A. (2019). Decomposing individual differences in cognitive control: A model-based approach. In A. K. Goel, C. M. Seifert, & C. Freksa (Eds.), *Proceedings of the 41st annual conference of the Cognitive Science Society* (pp. 2427–2433). Cognitive Science Society.

Musslick, S., Jang, J. S., Shvartsman, M., Shenhav, A., & Cohen, J. D. (2018). Constraints associated with cognitive control and the stability-flexibility dilemma. In T. T. Rogers, M. Rau, X. Zhu, & C. W. Kalish (Eds.), *Proceedings of the 40th annual conference of the Cognitive Science Society* (pp. 806–811). Cognitive Science Society.

Musslick, S., Saxe, A., Özcimder, K., Dey, B., Henselman, G., & Cohen, J. D. (2017). Multitasking capability versus learning efficiency in neural network architectures. In G. Gunzelmann, A. Howes, T. Tenbrink, & E. J. Davelaar (Eds.), *Proceedings of the 39th annual conference of the Cognitive Science Society* (pp. 829–834). Cognitive Science Society.

Niendam, T. A., Laird, A. R., Ray, K. L., Dean, Y. M., Glahn, D. C., & Carter, C. S. (2012). Meta-analytic evidence for a superordinate cognitive control network subserving diverse executive functions. *Cognitive, Affective & Behavioral Neuroscience*, *12*(2), 241–268. https://doi.org/10.3758/s13415-011-0083-5

Nolan, D. (1997). Quantitative parsimony. *The British Journal for the Philosophy of Science*, *48*(3), 329–343. https://doi.org/10.1093/bjps/48.3.329

Norman, D. A., & Shallice, T. (1986). Attention to action. In R. J. Davidson, G. E. Schwartz, & D. Shapiro (Eds.), *Consciousness and self-regulation: Advances in research and theory* (pp. 1–18). Springer. https://doi.org/10.1007/978-1-4757-0629-1_1

Obrist, P. A. (1976). Presidential Address, 1975. The cardiovascular-behavioral interaction—As it appears today. *Psychophysiology*, *13*(2), 95–107. https://doi.org/10.1111/j.1469-8986.1976.tb00081.x

Obrist, P. A. (1981). *Cardiovascular psychophysiology: A perspective*. Plenum Press. https://doi.org/10.1007/978-1-4684-8491-5

Obrist, P. A., Gaebelein, C. J., Teller, E. S., Langer, A. W., Grignolo, A., Light, K. C., & McCubbin, J. A. (1978). The relationship among heart rate, caratid dP/dt, and blood pressure in humans as a function of the type of stress. *Psychophysiology*, *15*(2), 102–115. https://doi.org/10.1111/j.1469-8986.1978.tb01344.x

Padmala, S., & Pessoa, L. (2011). Reward reduces conflict by enhancing attentional control and biasing visual cortical processing. *Journal of Cognitive Neuroscience*, *23*(11), 3419–3432. https://doi.org/10.1162/jocn_a_00011

Paolone, G., Lee, T. M., & Sarter, M. (2012). Time to pay attention: Attentional performance time-stamped prefrontal cholinergic activation, diurnality, and performance. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *32*(35), 12115–12128. https://doi.org/10.1523/JNEUROSCI.2271-12.2012

Parikh, V., Kozak, R., Martinez, V., & Sarter, M. (2007). Prefrontal acetylcholine release controls cue detection on multiple timescales. *Neuron*, *56*(1), 141–154. https://doi.org/10.1016/j.neuron.2007.08.025

Posner, M. I., & Snyder, C. R. R. (1975). Attention and cognitive control. In R. L. Solso (Ed.), *Information processing and cognition* (pp. 55–85). Erlbaum.

Preuschoff, K., 't Hart, B. M., & Einhäuser, W. (2011). Pupil dilation signals surprise: Evidence for noradrenaline's role in decision making. *Frontiers in Neuroscience*, *5*, Article 115. https://doi.org/10.3389/fnins.2011.00115

Rainville, P., Duncan, G. H., Price, D. D., Carrier, B., & Bushnell, M. C. (1997). Pain affect encoded in human anterior cingulate but not somatosensory cortex. *Science*, *277*(5328), 968–971. https://doi.org/10.1126/science.277.5328.968

Ratcliff, R. (1978). A theory of memory retrieval. *Psychological Review*, *85*(2), 59–108. https://doi.org/10.1037/0033-295X.85.2.59

Reuter-Lorenz, P. A., & Cappell, K. A. (2008). Neurocognitive aging and the compensation hypothesis. *Current Directions in Psychological Science*, *17*(3), 177–182. https://doi.org/10.1111/j.1467-8721.2008.00570.x

Richter, M., Friedrich, A., & Gendolla, G. H. E. (2008). Task difficulty effects on cardiac activity. *Psychophysiology*, *45*(5), 869–875. https://doi.org/10.1111/j.1469-8986.2008.00688.x

Richter, M., & Gendolla, G. H. E. (2006). Incentive effects on cardiovascular reactivity in active coping with unclear task difficulty. *International Journal of Psychophysiology*, *61*(2), 216–225. https://doi.org/10.1016/j.ijpsycho.2005.10.003

Richter, M., Gendolla, G. H. E., & Wright, R. A. (2016). Three decades of research on motivational intensity theory: What we have learned about effort and what we still don't know. *Advances in Motivation Science*, *3*, 149–168. https://doi.org/10.1016/bs.adms.2016.02.001

Robbins, T. W., Everitt, B. J., Marston, H. M., Wilkinson, J., Jones, G. H., & Page, K. J. (1989). Comparative effects of ibotenic acid- and quisqualic acid-induced lesions of the substantia innominata on attentional function in the rat: Further implications for the role of the cholinergic neurons of the nucleus basalis in cognitive processes. *Behavioural Brain Research*, *35*(3), 221–240. https://doi.org/10.1016/S0166-4328(89)80143-3

Salamone, J. D., Pardo, M., Yohn, S. E., López-Cruz, L., SanMiguel, N., & Correa, M. (2015). Mesolimbic dopamine and the regulation of motivated behavior. In E. H. Simpson & P. D. Balsam (Eds.), *Behavioral neuroscience of motivation* (Vol. 27, pp. 231–257). Springer International Publishing. https://doi.org/10.1007/7854_2015_383

Samuels, E. R., & Szabadi, E. (2008). Functional neuroanatomy of the noradrenergic locus coeruleus: Its roles in the regulation of arousal and autonomic function part II: Physiological and pharmacological manipulations and pathological alterations of locus coeruleus activity in humans. *Current Neuropharmacology*, *6*(3), 254–285. https://doi.org/10.2174/157015908785777193

Sarter, M., Gehring, W. J., & Kozak, R. (2006). More attention must be paid: The neurobiology of attentional effort. *Brain Research. Brain Research Reviews*, *51*(2), 145–160. https://doi.org/10.1016/j.brainresrev.2005.11.002

Sarter, M., & Lustig, C. (2020). Forebrain cholinergic signaling: Wired and phasic, not tonic, and causing behavior. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *40*(4), 712–719. https://doi.org/10.1523/JNEUROSCI.1305-19.2019

Sarter, M., Lustig, C., Blakely, R. D., & Koshy Cherian, A. (2016). Cholinergic genetics of visual attention: Human and mouse choline transporter capacity variants influence distractibility. *Journal of Physiology-Paris*, *110*(1–2), 10–18. https://doi.org/10.1016/j.jphysparis.2016.07.001

Sarter, M., Lustig, C., Howe, W. M., Gritton, H., & Berry, A. S. (2014). Deterministic functions of cortical acetylcholine. *European Journal of Neuroscience*, *39*(11), 1912–1920. https://doi.org/10.1111/ejn.12515

Sarter, M., & Parikh, V. (2005). Choline transporters, cholinergic transmission and cognition. *Nature Reviews Neuroscience*, *6*(1), 48–56. https://doi.org/10.1038/nrn1588

Sarter, M., Parikh, V., & Howe, W. M. (2009). Phasic acetylcholine release and the volume transmission hypothesis: Time to move on. *Nature Reviews Neuroscience*, *10*(5), 383–390. https://doi.org/10.1038/nrn2635

Saunders, B., Milyavskaya, M., & Inzlicht, M. (2015). What does cognitive control feel like? Effective and ineffective cognitive control is associated with divergent phenomenology. *Psychophysiology*, *52*(9), 1205–1217. https://doi.org/10.1111/psyp.12454

Schouppe, N., Braem, S., De Houwer, J., Silvetti, M., Verguts, T., Ridderinkhof, K. R., & Notebaert, W. (2015). No pain, no gain: The affective valence of congruency conditions changes following a successful response. *Cognitive, Affective & Behavioral Neuroscience*, *15*(1), 251–261. https://doi.org/10.3758/s13415-014-0318-3

Schultz, W., Dayan, P., & Montague, P. R. (1997). A neural substrate of prediction and reward. *Science*, *275*(5306), 1593–1599. https://doi.org/10.1126/science.275.5306.1593

Shackman, A. J., Salomons, T. V., Slagter, H. A., Fox, A. S., Winter, J. J., & Davidson, R. J. (2011). The integration of negative affect, pain and cognitive control in the cingulate cortex. *Nature Reviews Neuroscience*, *12*(3), 154–167. https://doi.org/10.1038/nrn2994

Shenhav, A., Botvinick, M. M., & Cohen, J. D. (2013). The expected value of control: An integrative theory of anterior cingulate cortex function. *Neuron*, *79*(2), 217–240. https://doi.org/10.1016/j.neuron.2013.07.007

Shenhav, A., Cohen, J. D., & Botvinick, M. M. (2016). Dorsal anterior cingulate cortex and the value of control. *Nature Neuroscience*, *19*(10), 1286–1291. https://doi.org/10.1038/nn.4384

Shenhav, A., Musslick, S., Lieder, F., Kool, W., Griffiths, T. L., Cohen, J. D., & Botvinick, M. M. (2017). Toward a rational and mechanistic account of mental effort. *Annual Review of Neuroscience*, *40*(1), 99–124. https://doi.org/10.1146/annurev-neuro-072116-031526

Shenhav, A., Straccia, M. A., Musslick, S., Cohen, J. D., & Botvinick, M. M. (2018). Dissociable neural mechanisms track evidence accumulation for selection of attention versus action. *Nature Communications*, *9*(1), Article 2485. https://doi.org/10.1038/s41467-018-04841-1

Shiffrin, R. M., & Schneider, W. (1977). Controlled and automatic human information processing: II. Perceptual learning, automatic attending and a general theory. *Psychological Review*, *84*(2), 127–190. https://doi.org/10.1037/0033-295X.84.2.127

Silvestrini, N. (2015). The effort-related cost of implicit pain. *Motivation Science*, *1*(3), 151–164. https://doi.org/10.1037/mot0000020

Silvestrini, N. (2017). Psychological and neural mechanisms associated with effort-related cardiovascular reactivity and cognitive control: An integrative approach. *International Journal of Psychophysiology*, *119*, 11–18. https://doi.org/10.1016/j.ijpsycho.2016.12.009

Silvestrini, N. (2018). On the implicit influence of pain cues on cognitive effort: Evidence from cardiovascular reactivity. *Biological Psychology*, *132*, 45–54. https://doi.org/10.1016/j.biopsycho.2017.11.002

Silvestrini, N., Chen, J.-I., Piché, M., Roy, M., Vachon-Presseau, E., Woo, C.-W., Wager, T. D., & Rainville, P. (2020). Distinct fMRI patterns colocalized in the cingulate cortex underlie the after-effects of cognitive control on pain. *NeuroImage*, *217*, Article 116898. https://doi.org/10.1016/j.neuroimage.2020.116898

Silvestrini, N., & Gendolla, G. H. E. (2019). Affect and cognitive control: Insights from research on effort mobilization. *International Journal of Psychophysiology*, *143*, 116–125. https://doi.org/10.1016/j.ijpsycho.2019.07.003

Silvetti, M., Alexander, W., Verguts, T., & Brown, J. W. (2014). From conflict management to reward-based decision making: Actors and critics in primate medial frontal cortex. *Neuroscience and Biobehavioral Reviews*, *46*(Pt. 1), 44–57. https://doi.org/10.1016/j.neubiorev.2013.11.003

Silvetti, M., Baldassarre, G., & Caligiore, D. (2019). A computational hypothesis on how serotonin regulates catecholamines in the pathogenesis of depressive apathy. In V. Cutsuridis (Ed.), *Multiscale models of brain disorders* (pp. 127–134). Springer International Publishing. https://doi.org/10.1007/978-3-030-18830-6_12

Silvetti, M., Seurinck, R., van Bochove, M. E., & Verguts, T. (2013). The influence of the noradrenergic system on optimal control of neural plasticity. *Frontiers in Behavioral Neuroscience*, *7*, Article 160. https://doi.org/10.3389/fnbeh.2013.00160

Silvetti, M., Seurinck, R., & Verguts, T. (2011). Value and prediction error in medial frontal cortex: Integrating the single-unit and systems levels of analysis. *Frontiers in Human Neuroscience*, *5*, Article 75. https://doi.org/10.3389/fnhum.2011.00075

Silvetti, M., Seurinck, R., & Verguts, T. (2013). Value and prediction error estimation account for volatility effects in ACC: A model-based fMRI study. *Cortex*, *49*(6), 1627–1635. https://doi.org/10.1016/j.cortex.2012.05.008

Silvetti, M., Vassena, E., Abrahamse, E., & Verguts, T. (2018). Dorsal anterior cingulate-brainstem ensemble as a reinforcement meta-learner. *PLoS Computational Biology*, *14*(8), Article e1006370. https://doi.org/10.1371/journal.pcbi.1006370

Smith, B. T., & Hess, T. M. (2015). The impact of motivation and task difficulty on resource engagement: Differential influences on cardiovascular responses of young and older adults. *Motivation Science*, *1*(1), 22–36. https://doi.org/10.1037/mot0000012

St. Peters, M., Demeter, E., Lustig, C., Bruno, J. P., & Sarter, M. (2011). Enhanced control of attention by stimulating mesolimbic-corticopetal cholinergic circuitry. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *31*(26), 9760–9771. https://doi.org/10.1523/JNEUROSCI.1902-11.2011

Sternberg, S. (1966). High-speed scanning in human memory. *Science*, *153*(3736), 652–654. https://doi.org/10.1126/science.153.3736.652

Towse, J. N., & Hitch, G. J. (1995). Is there a relationship between task demand and storage space in tests of working memory capacity? *The Quarterly Journal of Experimental Psychology Section A*, *48*(1), 108–124. https://doi.org/10.1080/14640749508401379

Treadway, M. T., Bossaller, N. A., Shelton, R. C., & Zald, D. H. (2012). Effort-based decision-making in major depressive disorder: A translational model of motivational anhedonia. *Journal of Abnormal Psychology*, *121*(3), 553–558. https://doi.org/10.1037/a0028813

Tzelgov, J., Henik, A., & Berger, J. (1992). Controlling Stroop effects by manipulating expectations for color words. *Memory & Cognition*, *20*(6), 727–735. https://doi.org/10.3758/BF03202722

Umemoto, A., & Holroyd, C. B. (2015). Task-specific effects of reward on task switching. *Psychological Research*, *79*(4), 698–707. https://doi.org/10.1007/s00426-014-0595-z

van der Wel, P., & van Steenbergen, H. (2018). Pupil dilation as an index of effort in cognitive control tasks: A review. *Psychonomic Bulletin & Review*, *25*(6), 2005–2015. https://doi.org/10.3758/s13423-018-1432-y

Van Snellenberg, J. X., Slifstein, M., Read, C., Weber, J., Thompson, J. L., Wager, T. D., Shohamy, D., Abi-Dargham, A., & Smith, E. E. (2015). Dynamic shifts in brain network activation during supracapacity working memory task performance. *Human Brain Mapping*, *36*(4), 1245–1264. https://doi.org/10.1002/hbm.22699

Varazzani, C., San-Galli, A., Gilardeau, S., & Bouret, S. (2015). Noradrenaline and dopamine neurons in the reward/effort trade-off: A direct electrophysiological comparison in behaving monkeys. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *35*(20), 7866–7877. https://doi.org/10.1523/JNEUROSCI.0454-15.2015

Vassena, E., Deraeve, J., & Alexander, W. H. (2017). Predicting motivation: Computational models of PFC can explain neural coding of motivation and effort-based decision-making in health and disease. *Journal of Cognitive Neuroscience*, *29*(10), 1633–1645. https://doi.org/10.1162/jocn_a_01160

Vassena, E., Deraeve, J., & Alexander, W. H. (2019). Task-specific prioritization of reward and effort information: Novel insights from behavior and computational modeling. *Cognitive, Affective & Behavioral Neuroscience*, *19*(3), 619–636. https://doi.org/10.3758/s13415-018-00685-w

Vassena, E., Holroyd, C. B., & Alexander, W. H. (2017). Computational models of anterior cingulate cortex: At the crossroads between prediction and effort. *Frontiers in Neuroscience*, *11*, Article 316. https://doi.org/10.3389/fnins.2017.00316

Vassena, E., Krebs, R. M., Silvetti, M., Fias, W., & Verguts, T. (2014). Dissociating contributions of ACC and vmPFC in reward prediction, outcome, and choice. *Neuropsychologia*, *59*, 112–123. https://doi.org/10.1016/j.neuropsychologia.2014.04.019

Vassena, E., Silvetti, M., Boehler, C. N., Achten, E., Fias, W., & Verguts, T. (2014). Overlapping neural systems represent cognitive effort and reward anticipation. *PLOS ONE*, *9*(3), Article e91008. https://doi.org/10.1371/journal.pone.0091008

Verguts, T., Vassena, E., & Silvetti, M. (2015). Adaptive effort investment in cognitive and physical tasks: A neurocomputational model. *Frontiers in Behavioral Neuroscience*, *9*, Article 57. https://doi.org/10.3389/fnbeh.2015.00057

Vermeylen, L., Wisniewski, D., González-García, C., Hoofs, V., Notebaert, W., & Braem, S. (2020). Shared neural representations of cognitive conflict and negative affect in the medial frontal cortex. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *40*(45), 8715–8725. https://doi.org/10.1523/JNEUROSCI.1744-20.2020

Wager, T. D., Atlas, L. Y., Botvinick, M. M., Chang, L. J., Coghill, R. C., Davis, K. D., Iannetti, G. D., Poldrack, R. A., Shackman, A. J., & Yarkoni, T. (2016). Pain in the ACC? *Proceedings of the National Academy of Sciences of the United States of America*, *113*(18), E2474–E2475. https://doi.org/10.1073/pnas.1600282113

Walton, M. E., Groves, J., Jennings, K. A., Croxson, P. L., Sharp, T., Rushworth, M. F. S., & Bannerman, D. M. (2009). Comparing the role of the anterior cingulate cortex and 6-hydroxydopamine nucleus accumbens lesions on operant effort-based decision making. *European Journal of Neuroscience*, *29*(8), 1678–1691. https://doi.org/10.1111/j.1460-9568.2009.06726.x

Westbrook, A., & Braver, T. S. (2015). Cognitive effort: A neuroeconomic approach. *Cognitive, Affective & Behavioral Neuroscience*, *15*(2), 395–415. https://doi.org/10.3758/s13415-015-0334-y

Wright, R. A. (1996). Brehm's theory of motivation as a model of effort and cardiovascular response. In P. M. Gollwitzer & J. A. Bargh (Eds.), *The psychology of action: Linking cognition and motivation to behavior* (pp. 424–453). Guilford Press.

Wright, R. A. (1998). Ability perception and cardiovascular response to behavioral challenge. In M. Kofta, G. Weary, & G. Sedek (Eds.), *Personal control in action: Cognitive and motivational mechanisms* (pp. 197–232). Guilford. https://doi.org/10.1007/978-1-4757-2901-6_8

Wright, R. A. (2009). Drained: Studies of fatigue influence on engagement and associated cardiovascular responses. In L. Sher (Ed.), *Psychological factors and cardiovascular disorders: The role of stress and psychosocial influences* (pp. 195–212). Nova Science Publishers.

Wright, R. A., & Kirby, L. D. (2001). Effort determination of cardiovascular response: An integrative analysis with applications in social psychology. In M. P. Zanna (Ed.), *Advances in experimental social psychology* (Vol. 33, pp. 255–307). Academic Press. https://doi.org/10.1016/S0065-2601(01)80007-1

Wright, R. A., & Mlynski, C. (2019). Fatigue determination of inhibitory strength and control: A babe in a bath. *Motivation Science*, *5*(1), 66–78. https://doi.org/10.1037/mot0000114

Wright, R. A., & Stewart, C. C. (2012). Multifaceted effects of fatigue on effort and associated cardiovascular responses. In R. A. Wright & G. H. E. Gendolla (Eds.), *How motivation affects cardiovascular response: Mechanisms and applications* (pp. 199–218). American Psychological Association. https://doi.org/10.1037/13090-010

Zénon, A., Solopchuk, O., & Pezzulo, G. (2019). An information-theoretic perspective on the costs of cognition. *Neuropsychologia*, *123*, 5–18. https://doi.org/10.1016/j.neuropsychologia.2018.09.013

Received September 2, 2021
Revision received March 16, 2022
Accepted April 20, 2022 ■