CHAPTER

Sleep deprivation, effort allocation and performance

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Abstract

Sleep deprivation causes physiological alterations (e.g., decreased arousal, intrusion of microsleeps), that negatively affect performance on a wide range of cognitive domains. These effects indicate that cognitive performance relies on a capacity-limited system that may be more challenged in the absence of sleep. Additionally, sleep loss can result in a lower willingness to exert effort in the pursuit of performance goals. Such deficits in motivation may interact with the effects of capacity limitations to further stifle cognitive performance. When sleep-deprived, cognitive performance is experienced as more effortful, and intrinsic motivation to perform dwindles. On the other hand, increasing motivation extrinsically (e.g., by monetary incentives) can inspire individuals to allocate more task-related effort, and can partially counter performance deficits associated with sleep deprivation. In this chapter, we review current research on the interplay between sleep deprivation, effort and performance. We integrate these findings into an effort-based decision-making framework in which sleep-related performance impairments may result from a voluntary decision to withdraw effort. We conclude with practical implications of this framework for performance in healthy populations (e.g., work productivity) and clinical conditions.

Keywords

Sleep deprivation, Motivation, Effort, Reward, Performance, Decision-making

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1 Introduction

Sleep loss has profound negative effects on performance, with meta-analysis showing effects across multiple cognitive domains both from total sleep deprivation (Lim and Dinges, 2010; Pilcher and Huffcutt, 1996) and from short-term sleep restriction (Banks and Dinges, 2007; Lowe et al., 2017). A large body of research has evaluated situational factors (e.g., duration of prior wakefulness) and individual factors (e.g., physiological, genetic, or chronotype differences) that influence the degree of impairment related to sleep deprivation. Moreover, the effect of sleep deprivation seems to be partially dependent on the task an individual performs. The largest deficits are observed on measures of alertness and attention, with smaller and less consistent deficits in more complex tasks such as tests of crystallized intelligence, executive functions, and problem-solving (Lim and Dinges, 2010; Lowe et al., 2017).

Sleep deprivation brings about physiological changes that are likely to interfere with the efficiency of cognitive processes (e.g., decreased arousal, intrusion of micro-sleeps). The observed deficits in cognitive performance are therefore commonly interpreted as a reduction in the capacity to perform. A growing body of literature, however, indicates that besides these perturbations in cognitive capacity, motivational factors may influence how much cognitive performance is affected (Engle-Friedman, 2014). Optimal performance is critically dependent on the engagement of sufficient processing resources. It is proposed that when one is motivated to perform (intrinsically or extrinsically), declines in arousal could be partially rescued by the exertion of effort.

In this chapter, we review the current literature linking cognitive performance under sleep deprivation to shifts in effort expenditure. In particular, we will discuss how sleep deprivation alters the subjective evaluation of effort, how motivational manipulations may alter sleep deprived performance and physiology, and how shifted preference drives individuals to select lower effort strategies during sleep deprivation. We will furthermore discuss the neural systems that are proposed to underlie the decision to expend effort, and how they are affected by sleep deprivation. In particular, we will link the findings from sleep deprivation studies to a neuro-economic framework of effort-based decision-making.

2 Perspectives on sleep deprivation and effort

Several theories have advanced the notion that, under sleep-deprived conditions, the maintenance of performance is partially under voluntary control. For example, Kjellberg (1977) proposed that the negative effects of sleep deprivation on performance were largely due to decreasing arousal. While some task characteristics may potentiate the decline in arousal (e.g., long task duration, or task monotony), other features may counter this by increasing motivation (e.g., providing performance feedback). Under such motivated conditions performance decrements were found to be much less steep than in non-motivated conditions (Wilkinson, 1961). In a related account, Sanders (1983) proposed that effort exertion can energize cognitive and motor processes, thereby up-regulating arousal and motor activation. This model further describes that increased effort could enhance performance at different processing stages (i.e., by facilitating stimulus processing, response selection, or motor execution). In addition to declining arousal, Engle-Friedman (2014) describes that sleep loss decreases the availability of energetical resources necessary to perform. Consequently, maintaining performance can become increasingly demanding, leading to an increased self-perceived effort.

A third model, by Monk (2012), proposes that the loss of motivation under sleep-deprived conditions could be an important factor that directly contributes to dwindling performance. Sleep deprivation may lead to increased negative mood, and to reduced willingness to perform. In conditions in which incentives are high to perform, e.g., in military emergency situations, people may be able to maintain performance. However, situations that do not contain significant extrinsic incentives may fail to generate sufficient motivation—and thus lead to reduced performance. Relatedly, the Compensatory Control Theory (Hockey, 1997), or Motivational Control Theory (Hockey, 2011, 2013), describes the allocation of effort as an adaptive decision process. Specifically, it claims that performance priorities may shift under suboptimal conditions like sleep deprivation. While under normal conditions, performance goals may be readily attained by exploiting lower-level non-costly processes, under sleep deprivation, this may only be possible by mobilizing compensatory effort. This effort may be experienced as a strain. Active monitoring systems would control how much effort would be allocated to performance maintenance, depending on the felt strain, and the goal value (i.e., importance of task). When effort exceeds a certain set-point, goal values might be adjusted downwards, resulting in poorer performance. Alternatively, if task goals are considered to be highly important, effort set-points can be adjusted, and additional effort can be mobilized in order to protect performance.

These models and the associated empirical research support the idea that performance decline under sleep deprivation is partly under voluntary control, and a shift in the motivation to perform may contribute to the observed effects. This line of thinking, however, has been criticized as motivation may not truly counter the underlying physiological changes brought about by sleep deprivation (Dinges and Kribbs, 1991). Compensatory effort may only rescue performance for a short while, and cognitive lapses during sleep deprivation occur even when the consequences of doing so are catastrophic (Dinges, 1995), indicating the need for a more nuanced examination of the role of motivation under sleep deprivation. Moreover, despite a vast literature on sleep deprivation, studies that systematically examine the interplay between sleep deprivation, motivation and performance remain relatively scarce. In contrast to this, the field of cognitive neuroscience has more actively studied motivation and effort, and their impact on performance. Over the last few decades, the field of cognitive neuroscience has seen a particularly steep growth in interest in this area (Braver et al., 2014). In the next section we will discuss these ideas about motivation and effort allocation from cognitive neuroscience (and the subfield of neuroeconomics in specific), and how they can be related to sleep deprivation.

3 Neuroeconomic perspectives on effort

In recent years, the field of cognitive neuroscience has shown a growing interest in how performance might result from a process of weighing the costs of effort against the value of performance goals. Similar ideas as described in the Compensatory Control Theory have been expressed in neuroeconomic theories (Chong et al., 2016; Kurzban et al., 2013; Pessiglione et al., 2017; Shenhav et al., 2017; Westbrook and Braver, 2015). In particular, it is proposed that cognitive operations carry intrinsic computational and energetic costs (Shenhav et al., 2017). That is, the computations underlying cognitive operations depend on the active recruitment of neural circuits. The recruitment of a larger pool of such neuronal resources may render such computations faster or more reliable, thereby improving cognitive performance (Zenon et al., 2019). However, increased neural activity requires increased energy expenditure, and is therefore thought to be metabolically costly (Christie and Schrater, 2015). These costs may be felt as effort (Boksem and Tops, 2008; Kurzban, 2016), and when possible, will be avoided or minimized (Kool et al., 2010). Under motivated conditions, the expense of costly cognitive operations may be justified (Botvinick and Braver, 2015), and compensatory resources may be deployed in order to enhance performance (Verguts et al., 2015). Importantly, performance output depends on a constant weighing of performance benefits (e.g., money) against associated costs (e.g., effort; Westbrook and Braver, 2015). If task goals carry a high value, more effort is allocated to performance. In contrast, when costs are high, individuals may withdraw effort from performance, and instead focus on alternative goals (e.g., taking a rest; Kurzban et al., 2013).

In this neuroeconomic framework, actions are seen as the outcome of a cost-benefit decision process (see Fig. 1). Central to this framework is the idea that the benefits that are associated with a choice (e.g., monetary reward or appreciation from one’s boss) are being discounted based on the costs associated (e.g., the effort or the time required, or the risk of failing to obtain the reward). In this way, a large reward (e.g., $100) may be worth less to a decision maker, if a high degree of effort is required. Accordingly, it may be equally preferred to accept a lower reward (e.g., $50), if that can be obtained with lesser effort. It is thought that decisions whether to pursue an action are based on the integration of these costs and benefits into a net subjective value, as formalized in a discounting function (Pessiglione et al., 2017):

$$\text{Subjective Value}\,[\text{action}_i] = \text{Reward}\,[\text{action}_i] - \text{Costs}\,[\text{action}_i]$$

The exact mathematical function that underlies discounting behavior is still debated, and may depend on the type of cost involved (i.e., effort, time, risk). However, the basic premise is that the costs associated with an option reduce the subjective value

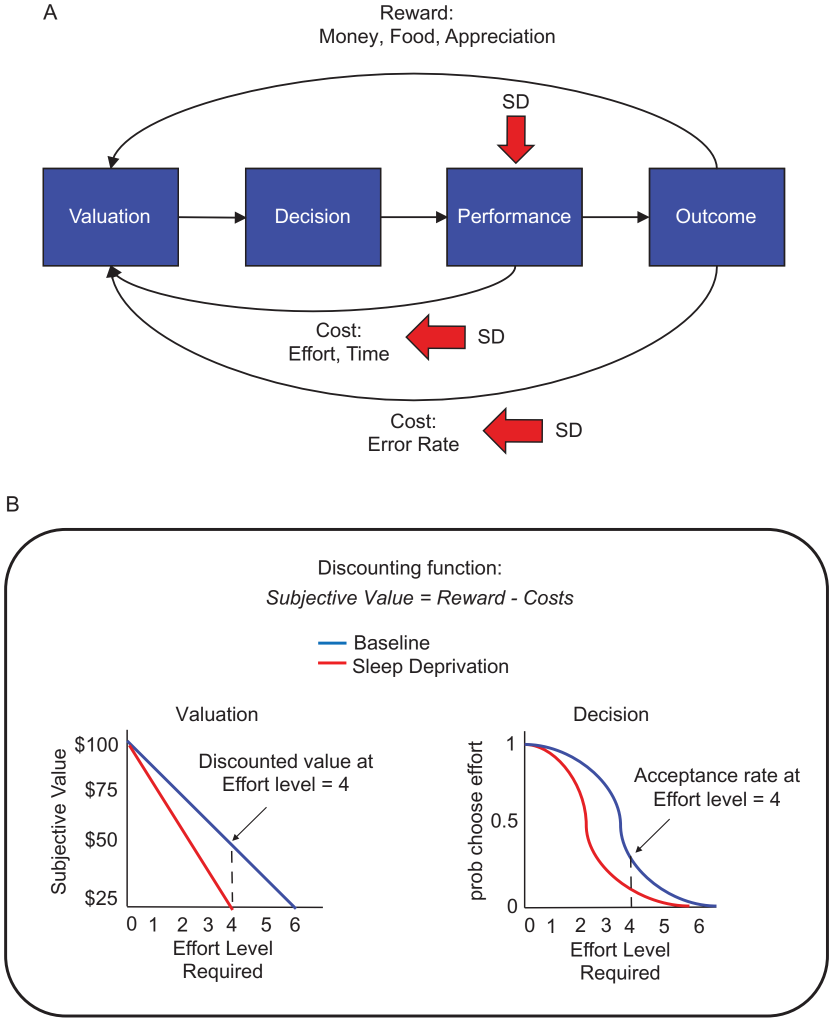

FIG. 1

(A) Schematic diagram of the cost-benefit decision process: at the Valuation stage, information about costs and benefits of the action options is integrated in a subjective value. These subjective values are compared and lead to a Decision on what action to engage in. The subsequent Performance provides information about costs and Outcome benefits that are used to update the value expectations. Red arrows indicate potential effects of sleep deprivation (SD), impaired performance, higher error rate and increased effort required may lead to stronger weighting of performance costs feeding back into the Valuation process. (B) Illustration of the discounting function showing the decreasing subjective value of a reward given increasing levels of effort required to obtain it (left panel), where stronger weighting of effort costs during sleep deprivation lead to steeper discounting, and (right panel) the probability of engaging in an effortful action given the effort level required and the associated subjective value under baseline and sleep deprived conditions.

of a reward, relative to its objective (e.g., dollar) value. Resulting subjective values for different action options (e.g., work versus taking a break) can be used to inform a decision on which action to perform (i.e., the action with the highest subjective value). Subsequently, monitoring of performance and its outcomes (e.g., effort/time required, performance accuracy, reward obtained) can act as feedback into the valuation process to update the subjective values associated with the potential actions. These processes may play out in succession or in parallel (Glimcher, 2009; Platt and Plassmann, 2014) to provide constant feedback about performance levels and the associated costs and benefits, that can be used to adjust performance goals, and the level of effort invested in the performance of a specific task (Boksem and Tops, 2008; Pessiglione et al., 2017).

Although the role of sleep deprivation is not explicitly discussed in these neuroeconomic models, it is widely recognized that bodily states (e.g., hunger or fatigue) can impact the decision process by altering the weighing of specific rewards (e.g., enhancing the value of high-caloric food rewards when one is hungry; Hare et al., 2009; Lee et al., 2013) or costs (e.g., increasing the weight of effort costs when one gets fatigued due to repeated exertion; Le Bouc et al., 2016). Following the motivational models of sleep deprivation, discussed in the previous section, it could be expected that in a sleep deprived state, performance would be associated with higher costs. Due to decline in arousal and energetic resources, performance would be slower and more prone to error (Engle-Friedman, 2014; Kjellberg, 1977; Sanders, 1983). Compensating these deficits to maintain high levels of performance may require high levels of effort (Engle-Friedman, 2014; Hockey, 2013). With increased costs, the subjective value of task performance may be discounted more steeply, and participants may be less inclined to invest effort into performance of a primary task. The neuroeconomic framework described in this section would lead to several predictions on the interaction between sleep deprivation performance and motivation. In the following sections we will discuss the existing empirical evidence for such interaction. We will discuss the motivational effects of sleep deprivation at the levels of subjective experience, performance and decision-making, respectively.

4 Sleep deprivation, subjective effort, and motivational reduction

If individuals weigh effort against rewards when tuning performance levels, then some internal evaluation processes must track the subjectively felt level of effort. This experienced effort is then registered as a cost, which leads to the discounting of associated rewards (Kurzban, 2016). Several studies on sleep deprivation have measured subjective effort through self-report. In a study by Pilcher and Walters (1997), participants performed a critical-thinking task for which they answered comprehension questions about a written text. Half of the participants performed this task after a normal night of sleep, and the other half was sleep deprived for one night. As expected, participants in the sleep deprivation group performed significantly worse and found the task more effortful than participants in the control group. Yet, contrary to their actual performance, participants in the sleep deprivation group judged their concentration to be higher and their performance to be better than did control participants. Hockey et al. (1998) similarly found that participants rated the effort needed to perform a complex machine operating task as higher when they were sleep deprived compared to when they were rested. Despite sleep deprivation, participants were able to maintain a high level of performance on a primary task (i.e., controlling air pressure and content in a simulated space cabin). However, execution of secondary maintenance tasks (e.g., periodically checking gas tank levels, and keeping an error log) was often mistimed or neglected while sleep deprived. This pattern of results may indicate that participants shifted priorities to performance on the primary task, and allocated processing resources accordingly.

The subjective experience of effort may differ by task type. Odle-Dusseau et al. (2010) examined the progression of subjective effort ratings over a night of sleep deprivation. Participants performed alternating blocks of a visuo-spatial tracking task and a vigilance task over a 5-h period (5:30–10:30 a.m.). With longer task duration (and consequently longer time awake), participants rated the required effort as progressively greater for both tasks. Importantly, this time-on-task increase was more strongly pronounced for the vigilance task compared to the tracking task. This may indicate that, in line with Kjellberg's (1977) model, sleep deprivation potentiates the de-arousing effects of the environment. As vigilance performance may be more conducive for loss of arousal than a more eventful tracking task, more effort may be required to maintain sufficient levels of arousal.

Along with greater perceived effort expenditure, sleep deprivation can result in changes in the intrinsic motivation to perform. In the study by Odle-Dusseau et al. (2010) subjective motivation was measured simultaneously with effort ratings. Throughout the night participants indicated to be more motivated to do the tracking task than the vigilance task. With longer time-on-task (and time awake), however, motivation decreased for both tasks. In a different study (Mikulincer et al., 1989) subjective motivation was measured over a period of 72 h of sleep deprivation. As with the above study, motivation to perform the task decreased over the first night of sleep deprivation. Moreover, motivation closely followed a circadian pattern, being lowest at the acrophase of the circadian sleep drive. This was particularly the case during the second night of sleep deprivation. During the third day of the sleep deprivation protocol, however, task motivation had returned back to near-baseline levels. The authors attributed this to the psychological effects of approaching the end of the protocol (end spurt effect). Notably, subjective motivation to do other, non-experimental activities only decreased as time awake progressed.

Two further studies reported mixed findings from the same study sample. Participants performed a memory task and a vigilance task once after a night sleep deprivation and once after a night of normal sleep. For the memory task, participants indicated to require more effort to perform the memory task after sleep deprivation, but still be equally motivated to perform (Drummond et al., 2005b). For the vigilance task, perceived effort was not different after sleep deprivation compared to normal sleep, but motivation was reduced (Drummond et al., 2005a). In contrast to the findings by Odle-Dusseau et al. (2010), here the vigilance task was done only once for 10 min.

In summary, sleep deprivation leads participants to rate task performance as more effortful while reducing motivation to perform. These altered subjective evaluations of effort and motivation, however, may not always occur in parallel, and may differ across tasks. Moreover, these motivational changes may rely much on the duration of sleep deprivation, time-on-task, and circadian phase. These studies shed light on the subjective experience of effort exertion during sleep deprivation, and give insight into the alterations in intrinsic motivation to perform. Performance may additionally be driven by external motivating factors (e.g., performance incentives). How sleep deprivation interacts with such direct manipulations of motivational drive will be discussed in the next section.

5 Sleep deprivation and motivated performance

Motivational incentives provide a powerful way to boost performance (Knutson et al., 2001). A host of studies have shown that when good performance is incentivized, participants can mobilize cognitive resources in order to improve performance (e.g., Chiew and Braver, 2013; Krebs and Woldorff, 2017; Locke and Braver, 2008). Such mobilization is evident from increased brain activation (Jimura et al., 2010), and from peripheral physiological measures such as cardiovascular reactivity (Richter and Gendolla, 2009) and pupil dilation (Kahneman and Peavler, 1969). Moreover, provision of reward can partially counter performance decrements due to fatigue (Boksem et al., 2006; Hopstaken et al., 2014). Surprisingly, however, only a few studies have investigated the effects of (monetary) rewards on performance during sleep deprivation.

In a study by Horne and Pettitt (1985), participants remained awake for 3 days and three nights. At set times throughout the protocol they performed an auditory vigilance task. One group of subjects was instructed that they could earn additional bonus payment if they performed well (1.5–5p per correct response; increasing over consecutive days), while another group did not receive bonus payment. Over the first day of sleep deprivation, the non-rewarded group showed a significant deterioration of performance. In contrast, the rewarded group performed just as well as a non-sleep-deprived control group. Over consecutive days, performance for the rewarded group did gradually decline, with performance being equally poor for the rewarded and non-rewarded groups after 3 days of sleep deprivation. This study demonstrates that performance can be reasonably maintained in short-term sleep deprivation if performance is incentivized. However, incentives seem ineffective once sleep debt has accumulated past a certain critical level.

Another study found that participants who were incentivized for correct responses in a flanker task performed better than participants who were not incentivized, both after sleep deprivation and after normal sleep (Hsieh et al., 2010).

As expected, performance was worse during sleep deprivation than after normal sleep in both groups, but participants in the incentivized group performed better in both sessions. Moreover, error-related electro-cortical brain potentials, reflective of active monitoring of task performance (Error-Related Negativity; ERN), were reduced after sleep deprivation in the non-incentivized group, but not in the incentivized group. Interestingly, when asked how much effort they had invested in task performance, participants in the incentivized group indicated to have exerted more effort after sleep deprivation compared to after normal sleep, while no sleep-related differences were found for participants in the non-incentivized group. This suggests that the maintenance of performance under sleep deprivation may rely on a prioritized allocation of effort to high-value task goals (Hockey, 2011).

A recent study looked in more detail at reward motivation at different incentive levels (Massar et al., 2019). Participants performed the Psychomotor Vigilance Test (PVT; Dinges and Powell, 1985) and could either earn 1, 5 or 15 cents (Singapore dollar) for each fast response (see Fig. 2, upper panel). As could be expected, response speed was slower after sleep deprivation than after normal sleep, and deteriorated with longer task duration (i.e., reflecting fatigue associated with maintaining vigilance). In addition, these effects were modulated by reward, such that the detrimental effects of sleep deprivation and time-on-task were reduced with higher reward levels.

Combined, these results demonstrate that performance degradation due to sleep loss can be (partially) countered by enhancing participants' motivation to perform. At the same time, there are limits to how far incentivized performance can counter fatigue. Under conditions of severe sleep deprivation there may be insufficient spare capacity to improve performance (Horne and Pettitt, 1985). Also, the value of reward may become less over time, when more reward has been accumulated (i.e., diminishing marginal utility; Pine et al., 2009). However, it seems that individuals can nevertheless regulate performance levels under sleep deprivation based on reward prospects.

A further indication of such reward-related regulation can be found in measures of physiological arousal. Massar et al. (2019) also monitored participants' pupil diameter during PVT performance to examine whether the observed effects of motivation on performance during sleep deprivation were mediated by changes in arousal (Kjellberg, 1977). Pupil size is known to covary with arousal through sympathetic and parasympathetic innervation (Lowenstein and Loewenfeld, 1964). During sleep deprivation, pupil size becomes smaller and more variable, reflecting sleep-state instability (Wilhelm et al., 1998). Pupil diameter has also long been thought to reflect attentional effort exertion (Kahneman, 1973). It scales with task difficulty, task motivation (Gergelyfi et al., 2015; Massar et al., 2016) and with perceived effort (Zenon et al., 2014). In the study by Massar et al. (2018), pupil diameter showed a very similar pattern as behavioral performance (see Fig. 2, lower panels). Pupil diameter decreased with time-on-task, in both the sleep deprivation session and after normal sleep (RW: Rested Wakefulness) runs. Moreover, in the sleep deprivation session, this time-on-task effect was modulated by reward, such that higher levels of arousal were maintained over the high reward run.

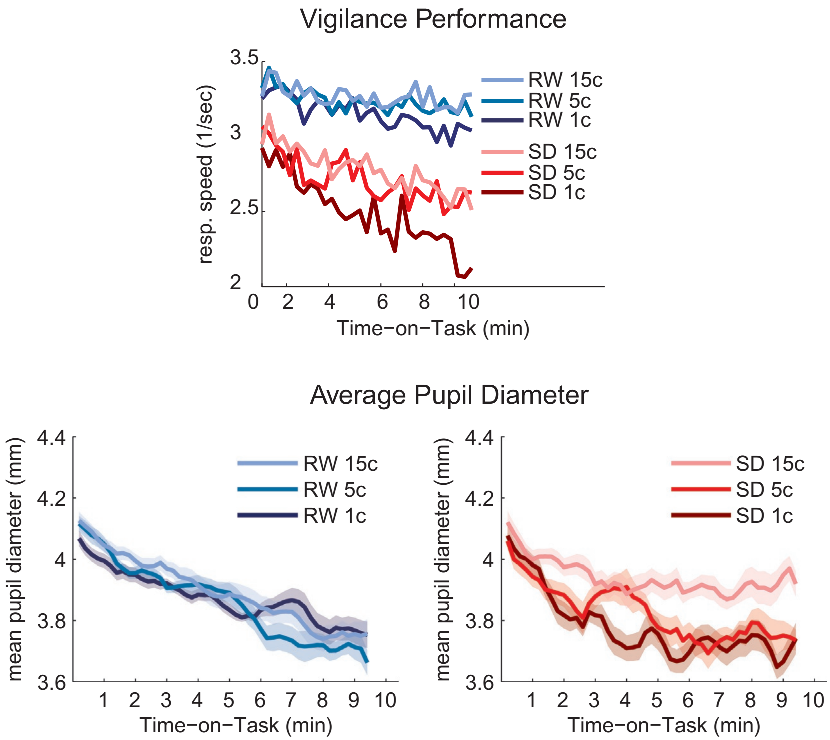

FIG. 2

Upper panel: Performance over the 10-min task runs of the Psychomotor Vigilance Test (PVT), during sleep deprivation (SD), and after normal sleep (RW: Rested Wakefulness). Lighter shade colors indicate higher incentive level (1c, 5c, or 15c per fast response). Lower panels: Pupil diameter over the 10-min task runs in the different sleep conditions and reward).

Adapted from Massar, S.A.A., Lim, J., Sasmita, K., Chee, M.W.L., 2019. Sleep deprivation increases the costs of attentional effort: performance, preference and pupil size. Neuropsychologia 123, 169–177.

Taken together, the above discussed studies on motivated performance show that enhancing motivation during sleep deprivation can aid to improve performance (at least temporarily). Motivation may generate cognitive or affective changes that counteract declines in arousal, leading to both improved performance and the experience of increased task-related effort.

6 Sleep deprivation and effort-based decision-making

The findings in motivated performance tasks indicate that individuals can (to some extent) exert more effort to improve performance when they are sufficiently incentivized. This implies that performance output relies in part on a decision process in which the costs of effortful performance are weighed against the potential benefits. Sleep deprivation could alter the reward value or the effort costs. Together, these in turn shape an individual's willingness to exert effort. Such effects can be examined directly by observing participants' choice behavior when different available courses of action are associated with different levels of effort (Kool et al., 2010; Shingledecker and Holding, 1974).

In a series of studies, Engle-Friedman and colleagues (Engle-Friedman and Riela, 2004; Engle-Friedman et al., 2003, 2008, 2010, 2018) explored how sleep loss would bias individuals' choices for effortful courses of action. In their Math Effort Task (MET), participants solved a series of mathematical problems (Engle-Friedman et al., 2003). Critically, on each trial participants could choose the difficulty level (1–5) of the problem to be solved. This essentially allowed the participants to freely choose the effort level that they preferred to pursue. Half of the sample underwent sleep deprivation, and the other half performed the MET after normal sleep. Throughout the task, sleep-deprived participants selected less difficult problems than the non-sleep-deprived group. Moreover, with longer time-on-task, the sleep-deprived group tended to choose less difficult problems. In another paradigm, the Activity Selection Task (AST), participants selected an activity that they would engage in for the next 20 min. Activities ranged from simple (e.g., retrieving voice messages or data entry) to difficult (e.g., composing exam questions or designing a research study). Sleep deprived participants chose significantly less difficult activities (Engle-Friedman et al., 2003). In two follow-up studies, naturally occurring differences in self-reported sleepiness and sleep quality on the previous night were predictive of the selected difficulty level in the MET (Engle-Friedman et al., 2008) and the AST (Engle-Friedman and Riela, 2004).

A different way of assessing the shift in preference for less effortful actions is through economic decision-making. In economic decision tasks, preferences associated with some factor (e.g., exertion of a given amount of effort) are quantified through examination of how that factor alters choices between monetary rewards (e.g., how much people pay to avoid expending effort). In one study, participants performed an effort-discounting task either after a night of sleep or after sleep deprivation in a counterbalanced within-subjects design (Libedinsky et al., 2013). Participants completed a series of choice trials (see Fig. 3A) in which they either could earn a large monetary reward in return for performing an effortful "backward typing" task, or alternatively could gain a smaller reward without any effort. The reward amount for the effortful option was always $20, while the smaller non-effortful reward varied on each trial ($1–$20). The required level of effort (i.e., the number of words to type) was also varied on each trial. After participants had made all their choices, one choice was randomly drawn. The participant received the indicated reward amount and would have to perform the chosen effort (type the indicated number of words). This procedure revealed that the subjective value of the effortful reward decreased with increasing effort levels (Fig. 3A, lower panels), such that participants considered a $20 reward less valuable if more effort was required to obtain it (i.e., they discounted the value of the reward). Critically,

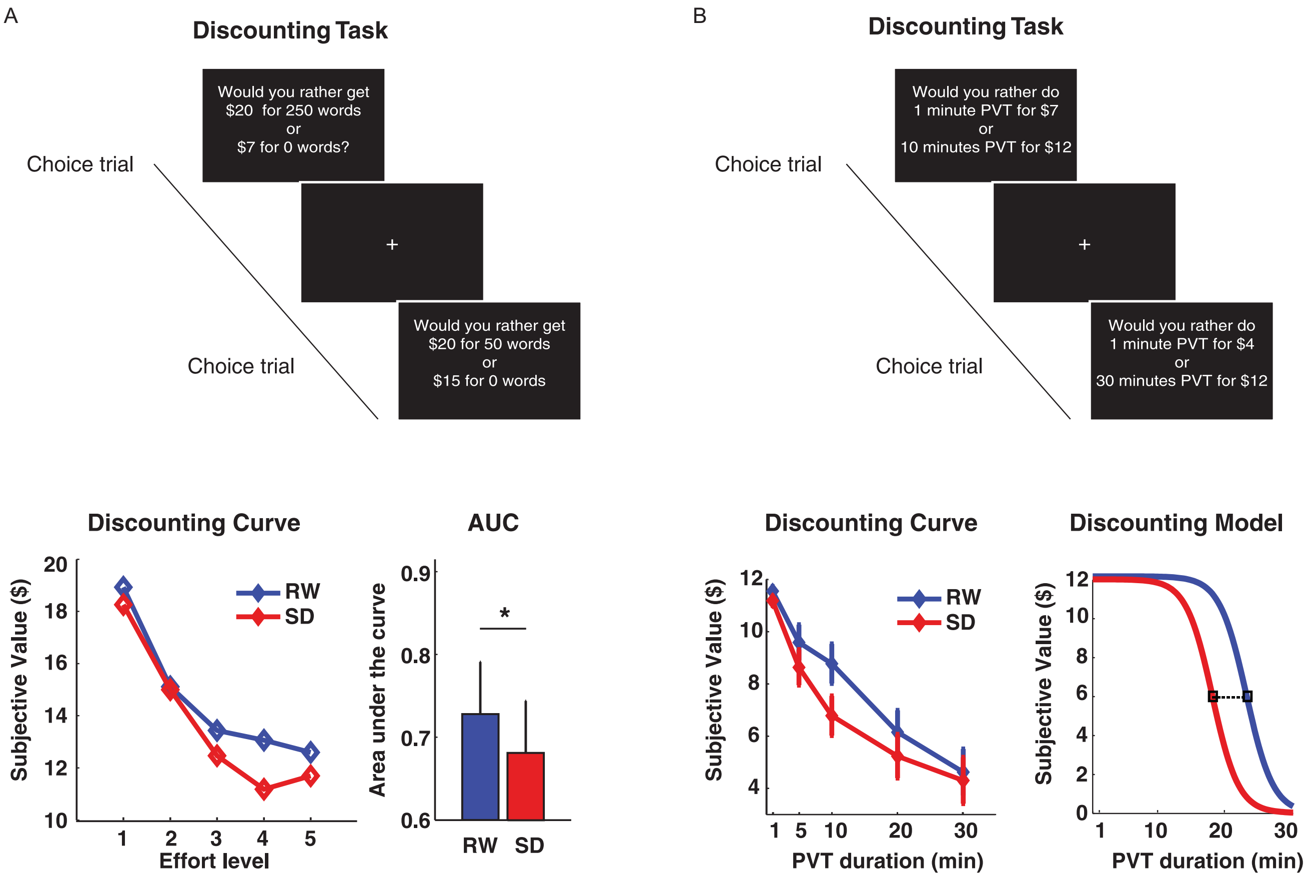

FIG. 3

Effort-discounting tasks and discounting curves after sleep deprivation (SD) and after normal sleep (RW: rested Wakefulness). (A) Upper panels: Exemplar trials in the choice tasks with effort operationalized as "backward word typing." Lower panels: Discounted value of a $20 reward at increasing effort levels, represented in the discounting curve (lower left panel), and quantified as the area under the discounting curve (AUC: lower right panel). (B) Effort operationalized as duration of sustained attention performance on the Psychomotor Vigilance Test (PVT). Lower panels: Discounted value of a $12 reward at increasing task durations, represented in the discounting curve (lower left panel), and modeled as the sigmoid discounting function (lower right panel).

Panel (A): Reconstructed based on data from Libedinsky, C., Massar, S.A.A., Ling, A., Chee, W.Y., Huettel, S.A., Chee, M.W.L., 2013. Sleep deprivation alters effort discounting but not delay discounting of monetary rewards. Sleep 36, 899–904.Panel (B): Adapted from Massar, S.A.A., Lim, J., Sasmita, K., Chee, M.W.L., 2019. Sleep deprivation increases the costs of attentional effort: performance, preference and pupil size. Neuropsychologia 123, 169–177.

discounting was more pronounced after sleep deprivation compared to normal sleep. This finding supports the idea that effort serves as a cost for economic decisions that is weighed more strongly when one is sleep deprived.

In a second study, a different discounting task was used to examine how sleep deprivation alters the subjective perception of effort involved in vigilance performance (Massar et al., 2019; see Fig. 3B). Participants were presented with a series of choice trials in which they decided between performing the PVT for a short duration (1 min) in return for a lower reward, or performing the PVT for a longer duration (5–30 min) for a larger reward ($12). As was found in the previously discussed study, subjective value was discounted for longer duration vigilance tasks (see Fig. 3B, lower panels). Using a computational modeling approach to fit the shape of the discounting curve, it was found that the devaluation of rewards followed a sigmoid function, which is more characteristic of effort-discounting than discounting based on other types of costs (e.g., time or risk; Klein-Flügge et al., 2015). Importantly, rewards were discounted at a higher rate (i.e., showing decreased subjective value for shorter task durations) after sleep deprivation compared to after normal sleep.

Overall, the cited studies demonstrate that during sleep deprivation, participants show a consistent shift in preference such that effortful activities are more frequently avoided, while associated rewards are more strongly discounted. This pattern applies to a range of different activities that are considered effortful (e.g., solving mathematics problems, prolonged vigilance performance) and aligns well with findings that these tasks are subjectively experienced as more effortful.

7 Neural correlates of effort-based decision-making

Making decisions about the value of an effortful course of action requires the integration of information about reward values with information about effort costs. Neuroimaging research has indicated that these functions are governed by two interacting systems. The first is the reward/valuation network, which comprises the ventral striatum (VS) and the ventromedial prefrontal cortex (vmPFC; for reviews, see Bartra et al., 2013; Clithero and Rangel, 2013). Activity in these two regions correlates with the value of offered rewards. The VS shows increased activation during motivated performance and anticipation of rewards (Croxson et al., 2009; Knutson et al., 2001). Furthermore, the VS is implicated in learning the expected value of choice options or actions during by calculating reward prediction errors during reinforcement learning (Dayan and Niv, 2008; Pessiglione et al., 2006; Schonberg et al., 2007). Activation in the vmPFC, in turn, integrates value information with cost information in the computation of a subjective value signal (Hare et al., 2009; Kable and Glimcher, 2007). It does so for different reward types (e.g., food, money or socially rewarding pictures; Chib et al., 2009; Levy and Glimcher, 2011; Smith et al., 2010), and for different decision domains (e.g., risk or intertemporal choice). It is therefore thought that value signals in the vmPFC facilitate decisions across reward and cost domains (Levy and Glimcher, 2012).

Information about the costs of effort, however, is found to be represented in a (partially) different set of brain areas (for reviews, see Chong et al., 2016; Le Heron et al., 2017; Pessiglione et al., 2017). Depending on the nature of the effortful action, effort costs can be encoded in task-specific areas (i.e., motor areas for physical effort tasks, and cognitive control areas for cognitive effort tasks; Schmidt et al., 2012). Furthermore, a more domain-general set of brain areas seems to encode for effort-costs across different types of effort. Chong et al. (2017) for instance, scanned participants while making choices about tasks that involved either cognitive effort (i.e., attentional switching) or physical effort (i.e., pressing a dynamometer; see Fig. 4A). They found that during decision-making, the subjective values of both the physical and cognitive effort tasks were represented in a common set of brain areas, including the dorsolateral prefrontal cortex (dlPFC), anterior insula (IA), and the dorsal anterior cingulate (dACC)/dorsomedial prefrontal cortex (dmPFC). Other studies have found similar areas involved in different effort tasks (Bonnelle et al., 2016; Klein-Flugge et al., 2016; Kurniawan et al., 2010; Meyniel et al., 2013). Moreover, a few studies have directly contrasted subjective valuation during effort-based decision-making with decision-making in other domains (e.g., probability or delay discounting), and found that these areas were uniquely involved in effort valuation (Burke et al., 2013; Massar et al., 2015; Prevost et al., 2010). Most early studies on effort-based decision-making did not find value encoding in the vmPFC, which would be expected based on findings in other decision domains. A growing body of literature however, has found evidence for the involvement of this area in effort-based valuation (Aridan et al., 2019; Arulpragasam et al., 2018; Hogan et al., 2018; Seaman et al., 2018). In particular, one study comparing decision-making across different decision domains (i.e., time, risk, effort), found that in a large sample of participants, subjective value in all domains was represented in an overlapping area in the vmPFC (Seaman et al., 2018). Other studies have implemented careful control conditions to isolate the valuation process and similarly found that activation levels in the vmPFC correlated with subjective value of effortful options (Arulpragasam et al., 2018; Hogan et al., 2018). It therefore seems likely that value computation in effort-based decision-making relies on an integration process in the vmPFC that is similar to that engaged in other decision domains.

Sleep deprivation alters these neural circuits for reward and effort in different ways. Firstly, several studies have shown higher overall activity of reward areas (VS and vmPFC), during the decision-making and consummatory stages of risk-based decision tasks, and reduced insula response after loss outcomes (Mullin et al., 2013; Venkatraman et al., 2007, 2011; See Fig. 3B). Furthermore, activation in the vmPFC has been found to less strongly correlate with subjective value during risky decisions after sleep deprivation (Menz et al., 2012), potentially related to shifted preferences (Libedinsky et al., 2011). Taken together, these changes under sleep deprivation may reflect a hypersensitivity to both the expectation and the receipt of reward, or a lower fidelity of processing of reward related information. None of these studies, however, included an effort manipulation.

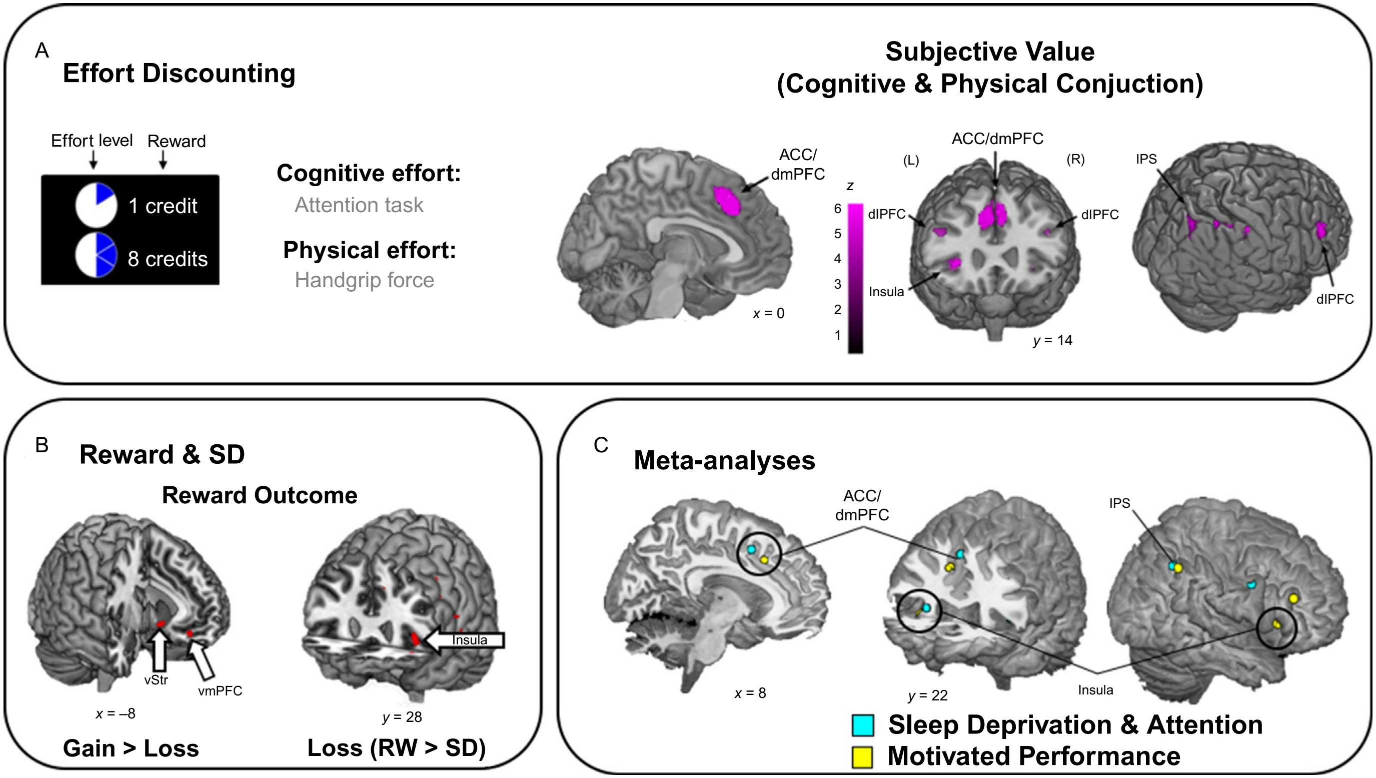

FIG. 4

(A) Neural correlates of subjective value encoding during effort-based decision-making. Markings in magenta indicate areas that code subjective value for both cognitive and for physically effortful tasks (ACC = anterior cingulate cortex; dmPFC = dorsomedial prefrontal cortex; dlPFC = dorsolateral prefrontal cortex; IPS = intraparietal sulcus). (B) Reward-related areas that show altered activation during sleep deprivation (SD = sleep deprivation; vStr = ventral striatum; vmPFC = ventromedial prefrontal cortex). (C) Comparison of brain areas that show reduced activation during attentional performance after sleep deprivation (cyan; peak foci from meta-analysis by Ma et al., 2015), and areas that show increased activation during motivated cognitive control performance (yellow; peak foci from meta-analysis by Parro et al., 2018).

Original figure 4A is licensed under CC BY 4.0.Panel (A): Adapted from 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 Biol. *15, e1002598-28 with permission.Panel (B): Adapted from Venkatraman, V., Huettel, S.A., Chuah, L.Y.M., Payne, J.W., Chee, M.W.L., 2011. Sleep deprivation biases the neural mechanisms underlying economic preferences. J. Neurosci. 31, 3712–3718.*

Therefore, it remains to be tested whether such sleep-related changes in the neural reward circuitry would generalize to the effort-based decision context.

Some clues about the potential neural interactions between effort and reward may be gleaned from studies in which participants maintain performance on other cognitive tasks while sleep deprived. While the exact brain areas affected by sleep deprivation may depend on the nature of the task at hand (e.g., visual processing areas for visual target detection tasks; Kong et al., 2014), some changes occur irrespective of task specifics. Remarkably, the areas that commonly show reduced activation during sleep-deprived performance also strongly overlap with the effort system highlighted above (Asplund and Chee, 2013; Chee et al., 2008; Lim et al., 2007). A meta-analysis including 11 neuroimaging studies on attention performance showed consistent decreased activation during sleep deprivation, in AI, and dlPFC areas as well as in the intraparietal sulcus (IPS; Ma et al., 2015). A different meta-analysis analyzing 16 studies on motivational control, indicates a highly similar set of brain areas, in which activation is upregulated during motived performance (Parro et al., 2018; See Fig. 3C for a comparison). In light of the role of these areas in encoding the value of effortful performance, it is tempting to think that reduced activation under sleep deprivation would reflect a shifted motivational value associated with attentional performance. However, a direct test of such a relationship between reduced activation during performance and altered effort-preference has not yet been reported.

8 What makes performance under sleep deprivation effortful?

We will now turn to the mechanisms by which sleep deprivation may make performance more effortful. One potential contributor could be the increased challenge to maintain arousal under sleep deprivation. As proposed in classical accounts by Kjellberg (1977) and Sanders (1983), increased sleep drive leads to a decline in arousal that can be countered by exertion of effort. An interesting finding in this respect is that in neuroimaging studies, sleep deprivation is consistently associated with increased thalamic activation (Ma et al., 2015). This hyperactivation has often been interpreted as reflecting the effort to stay awake (Thomas et al., 2000). Moreover, higher thalamic activation has been related to better performance after sleep deprivation (Chee and Tan, 2010). Pupillometric findings from Massar et al. (2019) show that after sleep deprivation, pupil size showed less decrease during task runs in which high incentives were at stake. This suggests that such effortful maintenance of arousal may be partially under motivational control.

Related to this, it has been shown that performance decline associated with sleep deprivation does not simply reflect an overall decline in arousal. Rather, periods of relative normal arousal are intermittently interrupted by brief periods of extremely low arousal (microsleeps). Microsleeps are characterized by physiological signs of sleep like increased slow wave EEG (Makeig et al., 2000), sharp pupil constriction (Wilhelm et al., 1998), and eye closures (Ong et al., 2013). Behaviorally, microsleeps are accompanied by extremely long RTs (lapses), leading to a pattern of behavioral instability (Doran et al., 2001). Whether the occurrence of microsleeps can be voluntarily counteracted can be debated. Pupillometric data from Massar et al. (2019) indicate that even in high reward task runs, short periods of very low arousal (small pupil diameter) alternate with moderate arousal states. Moreover, these low arousal periods were associated with particularly slow responses, suggesting that microsleep (and the associated behavioral lapsing) could not be fully prevented with increased motivation.

A third mechanism by which sleep deprivation may increase experienced effort is through the disruption of neural network function at a local scale (Chee et al., 2011). Under normal rested conditions, a given cognitive operation (e.g., maintaining a working memory representation over time) is supported by a network of multiple neuronal pools (see Fig. 5). Under conditions of sleep deprivation, some of these neuron pools may randomly switch to a sleep-like state, and become dysfunctional, while the remaining network nodes continue to support task performance This phenomenon is known as local sleep, and is thought to allow individual neurons to recuperate from prolonged activity, without the whole brain entering a state of sleep (local sleep; Vyazovskiy et al., 2011). Different from micro-sleep, the individual maintains the ability to perform in this situation. However, due to the random drop-out of functional nodes, cognitive operations become more erratic and more prone to noise (Poh and Chee, 2017). An interesting recent account of cognitive control has proposed that, under motivated conditions, network performance can be improved by increasing the number of active nodes involved in a cognitive operation at

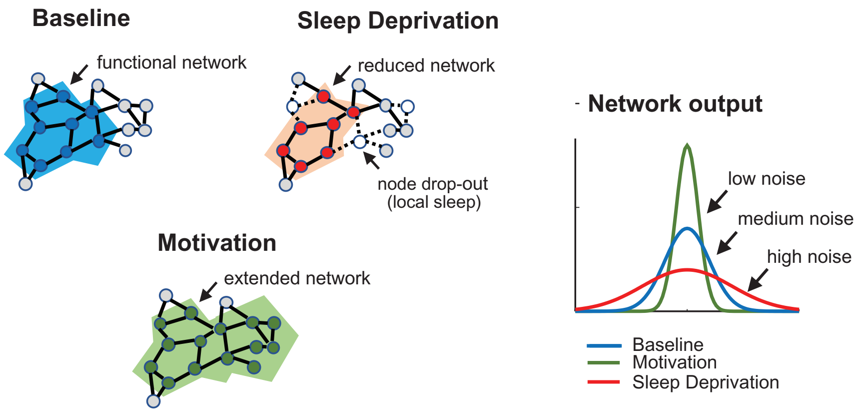

FIG. 5

Illustration of functional networks supporting cognitive performance in baseline, sleep deprived and motivated conditions. During sleep deprivation network size is reduced due to random drop-out of network nodes (local-sleep), resulting in higher noise. In motivated conditions, noise can be suppressed by recruiting a larger number of nodes into the functional network.

hand. Simultaneous engagement of multiple such assemblies can lead to improved performance by reducing the noise in the system (Manohar et al., 2015; Zenon et al., 2019). Performance improvements through this sort of redundancy would be metabolically costly, and optimal control depends on the weighing of such costs against potential benefits (Shenhav et al., 2013; Zenon et al., 2019). Maintenance of performance levels, therefore, may rely on activation of a larger number of functional nodes, in order to account for stochastic drop-out due to local sleep.

9 Limitations and practical relevance

The above sections summarize the evidence that maintaining performance during sleep deprivation is experienced as more effortful, more costly, such that associated rewards are discounted more steeply. Sleep deprivation may be associated with reduced functionality in neural circuits that support task performance and effort valuation. These findings provide converging support for motivational accounts of sleep deprivation (Engle-Friedman, 2014; Hockey, 1997; Kjellberg, 1977; Sanders, 1983) and align well with current ideas about effort allocation and motivation (Kool et al., 2010; Kurzban et al., 2013; Shenhav et al., 2017; Westbrook and Braver, 2015). Similar ideas have been expressed in a broader context of fatigue (Boksem and Tops, 2008; Dobryakova et al., 2013; Hockey, 2013; Kanfer and Ackerman, 1989; Massar et al., 2018; Müller and Apps, 2019).

Some limitations of a motivational account must be noted. As pointed out by Dinges and Kribbs (1991), motivation may not be sufficient to counter performance deficits at longer durations of wakefulness. Moreover, evidence for motivation-related decline does not imply that underlying physiological perturbations are not influential nor that deficits can be fully eradicated simply by increasing motivation. Evidence for such limits to the motivational account can be seen in the findings by Horne and Pettitt (1985), who found that incentives benefitted performance over the earlier part of a sleep deprivation protocol (up to 2 days of extended wakefulness). After that, accumulated sleep pressure may be too severe to volitionally counteract performance deterioration through effort mobilization. Clearly, reduced motivation for effort is not the whole story. Rather we argue that reduced willingness to exert effort may be an inherent, additional risk factor that contributes to impaired performance under sleep deprivation. Particularly, we would expect that performance is more sensitive to motivational decline under conditions of moderate sleep deprivation/restriction, when homeostatic sleep drive is not yet too severe.

So, what is the practical value of the motivational account of sleep deprivation? Instances of total sleep deprivation longer than 24 h are relatively rare; more common are repeated, shorter bouts of sleep restriction (Hafner et al., 2016). A recent large-scale survey reported that across five major economies, 19–40% of the workforce population slept between 6 and 7 h per night (short sleep), while 6–18% slept less than 6 h on average (very short sleep). Within these ranges, motivational deficits may have a substantial impact on work productivity, due to less focused or less efficient performance (Kühnel et al., 2017; Wagner et al., 2012). Even when work gets done, increased aversion to effort may lead people to choose less careful strategies to meet production targets (Shingledecker and Holding, 1974). This may come at the cost of increased risk of error and accidents. In the same way, shifts toward less effortful strategies may affect optimal athletic training performance (Barte et al., 2018; Engle-Friedman et al., 2010) and academic performance and motivation (Edens, 2006; Gatzke-Kopp et al., 2017).

The accrual of accumulated sleep debt is also a major problem in clinical sleep disorders such as insomnia. Interestingly, "daytime dysfunction," an essential element for insomnia diagnosis is often characterized by "reduced motivation, energy or initiative" (Krahn, 2007). A recent study reported that patients suffering from insomnia have lower self-ratings of motivational and hedonic valuation of rewards, compared to healthy control subjects (Te Lindert et al., 2018). These motivational ratings were more sensitive in distinguishing patients from controls than ratings of positive or negative mood. Other researchers have found that reward related brain responses individuals with sleep problems were cross-sectionally (Avinun et al., 2017), and prospectively correlated with depression symptoms (Casement et al., 2016). In line with these findings, it has been proposed that dysregulation of reward function, due to repeated and accumulative sleep disturbance, may increase longer-term vulnerability of developing mood and motivational disorder (Kalmbach et al., 2017; Perogamvros et al., 2013). Research on motivational deficits in sleep disorders is scarce. A few researchers have started to explore this link (Boland et al., 2019), but more work is needed to delineate whether and how motivation for effort could affect performance in these conditions. Given the chronic nature of sleep disturbance and the suggested role in the development of motivation-related pathology, we would see it as a particular important area for further investigation.

10 Conclusion

The literature reviewed in this chapter revealed several different ways in which motivation and effort allocation change after sleep deprivation. On a subjective level, sleep loss is accompanied by an increased perception of effort while performing a task, and reduction in a subject's motivation. Performance metrics show that impairments that are associated with sleep loss, can be countered if motivation is enhanced, e.g., by monetary incentives. At the same time, individuals weigh the required effort more strongly in their decisions to pursue a course of action, leading to fewer high effort choices, and a lower valuation of associated rewards. Perturbations in the function of brain circuits involved in task performance, reward valuation, and effort monitoring/regulation, may underlie the observed behavioral outcomes. These findings fit well in a framework of value-based effort allocation, indicating that motivational factors substantially contribute to performance decline under sleep loss. This conceptualization of effort allocation and motivation as critical factors in human performance under sleep deprivation and fatigue follows a long tradition of psychological theory. However, empirical studies on this area are still remarkably sparse. Gaining a better understanding of the interplay between sleep loss, motivation and effort allocation is relevant to a wide range of fields including industrial psychology, cognitive neuroscience, and clinical practice. Future studies should aim to further map motivational changes related to acute and chronic sleep loss, both in healthy and clinical populations.

References

Aridan, N., Malecek, N.J., Poldrack, R.A., Schonberg, T., 2019. Neural correlates of effort-based valuation with prospective choices. Neuroimage 185, 446–454.

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. Proc. Natl. Acad. Sci. U.S.A. 115, E5233–E5242.

Asplund, C.L., Chee, M.W.L., 2013. Time-on-task and sleep deprivation effects are evidenced in overlapping brain areas. Neuroimage 82, 326–335.

Avinun, R., Nevo, A., Knodt, A.R., Elliott, M.L., Radtke, S.R., Brigidi, B.D., Hariri, A.R., 2017. Reward-related ventral striatum activity buffers against the experience of depressive symptoms associated with sleep disturbances. J. Neurosci. 37, 9724–9729.

Banks, S., Dinges, D.F., 2007. Behavioral and physiological consequences of sleep restriction. J. Clin. Sleep Med. 3, 519–528.

Barte, J.C.M., Nieuwenhuys, A., Geurts, S.A.E., Kompier, M.a.J., 2018. Effects of fatigue on interception decisions in soccer. Int. J. Sport Exerc. Psychol. 619, 1–12.

Bartra, O., Mcguire, J.T., Kable, J.W., 2013. The valuation system: a coordinate-based meta-analysis of BOLD fMRI experiments examining neural correlates of subjective value. Neuroimage 76, 412–427.

Boksem, M.A.S., Tops, M., 2008. Mental fatigue: costs and benefits. Brain Res. Rev. 59, 125–139.

Boksem, M.A.S., Meijman, T.F., Lorist, M.M., 2006. Mental fatigue, motivation and action monitoring. Biol. Psychol. 72, 123–132.

Boland, E.M., Bertulis, K., Chen, S., Thase, M.E., Gehrman, P.R., 2019. Preliminary support for the role of reward relevant effort and chronotype in the depression/insomnia comorbidity. J. Affect. Disord. 242, 220–223.

Bonnelle, V., Manohar, S., Behrens, T., Husain, M., 2016. Individual differences in premotor brain systems underlie behavioral apathy. Cereb. Cortex 26, 807–819.

Botvinick, M., Braver, T., 2015. Motivation and cognitive control: from behavior to neural mechanism. Annu. Rev. Psychol. 66, 83–113.

Braver, T.S., Krug, M.K., Chiew, K.S., Kool, W., Westbrook, J.A., Clement, N.J., Adcock, R.A., Barch, D.M., Botvinick, M.M., Carver, C.S., Cools, R., Custers, R., Dickinson, A., Dweck, C.S., Fishbach, A., Gollwitzer, P.M., Hess, T.M., Isaacowitz, D.M., Mather, M., Murayama, K., Pessoa, L., Samanez-Larkin, G.L., Somerville, L.H., 2014. Mechanisms of motivation-cognition interaction: challenges and opportunities. Cogn. Affect. Behav. Neurosci. 14, 443–472.

Burke, C.J., Brunger, C., Kahnt, T., Park, S.Q., Tobler, P.N., 2013. Neural integration of risk and effort costs by the frontal pole: only upon request. J. Neurosci. 33, 1706–1713.

Casement, M.D., Keenan, K.E., Hipwell, A.E., Guyer, A.E., Forbes, E.E., 2016. Neural reward processing mediates the relationship between insomnia symptoms and depression in adolescence. Sleep 39, 439–447.

Chee, M.W.L., Tan, J.C., 2010. Lapsing when sleep deprived: neural activation characteristics of resistant and vulnerable individuals. Neuroimage 51, 835–843.

Chee, M.W.L., Tan, J.C., Zheng, H., Parimal, S., Weissman, D.H., Zagorodnov, V., Dinges, D.F., 2008. Lapsing during sleep deprivation is associated with distributed changes in brain activation. J. Neurosci. 28, 5519–5528.

Chee, M.W.L., Goh, C.S.F., Namburi, P., Parimal, S., Seidl, K.N., Kastner, S., 2011. Effects of sleep deprivation on cortical activation during directed attention in the absence and presence of visual stimuli. Neuroimage 58, 595–604.

Chib, V.S., Rangel, A., Shimojo, S., O'doherty, J.P., 2009. Evidence for a common representation of decision values for dissimilar goods in human ventromedial prefrontal cortex. J. Neurosci. 29, 12315–12320.

Chiew, K.S., Braver, T.S., 2013. Temporal dynamics of motivation-cognitive control interactions revealed by high-resolution pupillometry. Front. Psychol. 4, 15.

Chong, T.T.-J., Bonnelle, V., Husain, M., 2016. Quantifying motivation with effort-based decision-making paradigms in health and disease. Prog. Brain Res. 229, 71–100.

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 Biol. 15, e1002598-28.

Christie, S.T., Schrater, P., 2015. Cognitive cost as dynamic allocation of energetic resources. Front. Neurosci. 9, 1–15.

Clithero, J.A., Rangel, A., 2013. Informatic parcellation of the network involved in the computation of subjective value. Soc. Cogn. Affect. Neurosci. 9, 1289–1302.

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. J. Neurosci. 29, 4531–4541.

Dayan, P., Niv, Y., 2008. Reinforcement learning: the good, the bad and the ugly. Curr. Opin. Neurobiol. 18, 185–196.

Dinges, D.F., 1995. An overview of sleepiness and accidents. J. Sleep Res. 4, 4–14.

Dinges, D.F., Kribbs, N.B., 1991. Performing while sleepy: effects of experimentally-induced sleepiness. In: Monk, T.H. (Ed.), Sleep, Sleepiness and Performance. John Wiley & Sons Ltd., Chichester, West Sussex, pp. 97–128.

Dinges, D.F., Powell, J.W., 1985. Microcomputer analyses of performance on a portable, simple visual RT task during sustained operations. Behav. Res. Methods Instrum. Comput. 17, 652–655.

Dobryakova, E., Deluca, J., Genova, H.M., Wylie, G.R., 2013. Neural correlates of cognitive fatigue: cortico-striatal circuitry and effort-reward imbalance. J. Int. Neuropsychol. Soc. 19, 849–853.

Doran, S.M., Van Dongen, H.P.A., Dinges, D.F., 2001. Sustained attention performance during sleep deprivation: evidence of state instability. Arch. Ital. Biol. 139, 253–267.

Drummond, S.P.A., Bischoff-Grethe, A., Dinges, D.F., Ayalon, L., Mednick, S.C., Meloy, M.J., 2005a. The neural basis of the psychomotor vigilance task. Sleep 28, 1059–1068.

Drummond, S.P.A., Meloy, M.J., Yanagi, M.A., Orff, H.J., Brown, G.G., 2005b. Compensatory recruitment after sleep deprivation and the relationship with performance. Psychiatry Res. Neuroimaging 140, 211–223.

Edens, K.M., 2006. The relationship of university students' sleep habits and academic motivation. J. Stud. Aff. Res. Pract. 43, 432–445.

Engle-Friedman, M., 2014. The effects of sleep loss on capacity and effort. Sleep Sci. 7, 213–224.

Engle-Friedman, M., Riela, S., 2004. Self-imposed sleep loss, sleepiness, effort and performance. Sleep Hypn. 6, 155–162.

Engle-Friedman, M., Riela, S., Golan, R., Ventuneac, A.M., Davis, C.M., Jefferson, A.D., Major, D., 2003. The effect of sleep loss on next day effort. J. Sleep Res. 12, 113–124.

Engle-Friedman, M., Riela, S., Strothers, E., 2008. Objective and subjective effort as a function of sleep and energy. Sleep Hypn. 10, 61–72.

Engle-Friedman, M., Palencar, V., Riela, S., 2010. Sleep and effort in adolescent athletes. J. Child Health Care 14, 131–141.

Engle-Friedman, M., Mathew, G.M., Martinova, A., Armstrong, F., Konstantinov, V., 2018. The role of sleep deprivation and fatigue in the perception of task difficulty and use of heuristics. Sleep Sci. 11, 74–84.

Gatzke-Kopp, L.M., Ram, N., Lydon-Staley, D.M., Dupuis, D., 2017. Children's sensitivity to cost and reward in decision making across distinct domains of probability, effort, and delay. J. Behav. Decis. Mak. 31, 12–24.

Gergelyfi, M., Jacob, B., Olivier, E., Zenon, A., 2015. Dissociation between mental fatigue and motivational state during prolonged mental activity. Front. Behav. Neurosci. 9, 176.

Glimcher, P.W., 2009. Choice: towards a standard back-pocket model. In: Glimcher, P.W., Camerer, C.F., Fehr, E., Poldrack, R.A. (Eds.), Neuroeconomics: Decision Making and the Brain, first ed. Academic Press, London, pp. 503–522.

Hafner, M., Stepanek, M., Taylor, J., Troxel, W.M., Van Stolk, C., 2016. Why Sleep Matters—The Economic Costs of Insufficient Sleep. Rand Europe, Cambridge.

Hare, T.A., Camerer, C.F., Rangel, A., 2009. Self-control in decision-making involves modulation of the vmPFC valuation system. Science 324, 646–648.

Hockey, G.R., 1997. Compensatory control in the regulation of human performance under stress and high workload; a cognitive-energetical framework. Biol. Psychol. 45, 73–93.

Hockey, G.R., 2011. A motivational control theory of cognitive fatigue. In: Ackerman, P.L. (Ed.), Cognitive Fatigue: Multidisciplinary Perspectives on Current Research and Future Applications. American Psychological Association, Washington, DC, pp. 167–187.

Hockey, G.R., 2013. The Psychology of Fatigue: Work, Effort and Control. Cambridge University Press, Cambridge.

Hockey, G.R., Wastell, D.G., Sauer, J., 1998. Effects of sleep deprivation and user interface on complex performance: a multilevel analysis of compensatory control. Hum. Factors 40, 233–253.

Hogan, P.S., Galaro, J.K., Chib, V.S., 2018. Roles of ventromedial prefrontal cortex and anterior cingulate in subjective valuation of prospective effort. Cereb. Cortex (in press).

Hopstaken, J.F., Van Der Linden, D., Bakker, A.B., Kompier, M.A.J., 2014. A multifaceted investigation of the link between mental fatigue and task disengagement. Psychophysiology 52, 305–315.

Horne, J.A., Pettitt, A.N., 1985. High incentive effects on vigilance performance during 72 hours of total sleep deprivation. Acta Psychol. (Amst) 58, 123–139.

Hsieh, S., Li, T.H., Tsai, L.L., 2010. Impact of monetary incentives on cognitive performance and error monitoring following sleep deprivation. Sleep 33, 499–507.

Jimura, K., Locke, H.S., Braver, T.S., 2010. Prefrontal cortex mediation of cognitive enhancement in rewarding motivational contexts. Proc. Natl. Acad. Sci. U.S.A. 107, 8871–8876.

Kable, J.W., Glimcher, P.W., 2007. The neural correlates of subjective value during intertemporal choice. Nat. Neurosci. 10, 1625–1633.

Kahneman, D., 1973. Attention and Effort. Prentice-Hall, Inc, Englewood Cliffs, New Jersey.

Kahneman, D., Peavler, W.S., 1969. Incentive effects and pupillary changes in association learning. J. Exp. Psychol. 79, 312–318.

Kalmbach, D.A., Arnedt, J.T., Swanson, L.M., Rapier, J.L., Ciesla, J.A., 2017. Reciprocal dynamics between self-rated sleep and symptoms of depression and anxiety in young adult women: a 14-day diary study. Sleep Med. 33, 6–12.

Kanfer, R., Ackerman, P.L., 1989. Motivation and cognitive abilities: an integrative/aptitude-treatment interaction approach to skill acquisition. J. Appl. Psychol. 74, 657–690.

Kjellberg, A., 1977. In: Mackie, R.R. (Ed.), Sleep Deprivation, Arousal, and Performance. Plenum, pp. 529–535.

Klein-Flügge, M.C., Kennerley, S.W., Saraiva, A.C., Penny, W.D., Bestmann, S., 2015. Behavioral modeling of human choices reveals dissociable effects of physical effort and temporal delay on reward devaluation. PLoS Comput. Biol. 11, e1004116.

Klein-Flugge, 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. J. Neurosci. 36, 10002–10015.

Knutson, B., Adams, C.M., Fong, G.W., Hommer, D., 2001. Anticipation of increasing monetary reward selectively recruits nucleus accumbens. J. Neurosci. 21, RC159.

Kong, D., Asplund, C.L., Chee, M.W.L., 2014. Sleep deprivation reduces the rate of rapid picture processing. Neuroimage 91, 169–176.

Kool, W., Mcguire, J.T., Rosen, Z.B., Botvinick, M.M., 2010. Decision making and the avoidance of cognitive demand. J. Exp. Psychol. Gen. 139, 665–682.

Krahn, L.E., 2007. Insomnia: differential pearls. In: Avidan, A., Barkoukis, T. (Eds.), Review of Sleep Medicine. Butterworth-Heinemann, pp. 95–104.

Krebs, R.M., Woldorff, M.G., 2017. Cognitive control and reward. In: Egner, T. (Ed.), The Wiley Handbook of Cognitive Control. John Wiley & Sons, Chichester, West Sussex, UK, pp. 422–439.

Kühnel, J., Sonnentag, S., Bledow, R., Melchers, K.G., 2017. The relevance of sleep and circadian misalignment for procrastination among shift workers. J. Occup. Organ. Psychol. 91, 110–133.

Kurniawan, I.T., Seymour, B., Talmi, D., Yoshida, W., Chater, N., Dolan, R.J., 2010. Choosing to make an effort: the role of striatum in signaling physical effort of a chosen action. J. Neurophysiol. 104, 313–321.

Kurzban, R., 2016. The sense of effort. Curr. Opin. Psychol. 7, 67–70.

Kurzban, R., Duckworth, A., Kable, J.W., Myers, J., 2013. An opportunity cost model of subjective effort and task performance. Behav. Brain Sci. 36, 661–679.

Le Bouc, R., Rigoux, L., Schmidt, L., Degos, B., Welter, M.L., Vidailhet, M., Daunizeau, J., Pessiglione, M., 2016. Computational dissection of dopamine motor and motivational functions in humans. J. Neurosci. 36, 6623–6633.

Le Heron, C., Apps, M.A.J., Husain, M., 2017. The anatomy of apathy: a neurocognitive framework for amotivated behaviour. Neuropsychologia 118, 54–67.

Lee, Y., Chong, M.F.-F., Liu, J.C., Libedinsky, C., Gooley, J.J., Chen, S., Wu, T., Tan, V., Zhou, M., Meaney, M.J., Lee, Y.S., Chee, M.W.L., 2013. Dietary disinhibition modulates neural valuation of food in the fed and fasted states. Am. J. Clin. Nutr. 97, 919–925.

Levy, D.J., Glimcher, P.W., 2011. Comparing apples and oranges: using reward-specific and reward-general subjective value representation in the brain. J. Neurosci. 31, 14693–14707.

Levy, D.J., Glimcher, P.W., 2012. The root of all value: a neural common currency for choice. Curr. Opin. Neurobiol. 22, 1027–1038.

Libedinsky, C., Smith, D.V., Teng, C.S., Namburi, P., Chen, V.W., Huettel, S.A., Chee, M.W. L., 2011. Sleep deprivation alters valuation signals in the ventromedial prefrontal cortex. Front. Behav. Neurosci. 5, 70.

Libedinsky, C., Massar, S.A.A., Ling, A., Chee, W.Y., Huettel, S.A., Chee, M.W.L., 2013. Sleep deprivation alters effort discounting but not delay discounting of monetary rewards. Sleep 36, 899–904.

Lim, J., Dinges, D.F., 2010. A meta-analysis of the impact of short-term sleep deprivation on cognitive variables. Psychol. Bull. 136, 375–389.

Lim, J., Choo, W.-C., Chee, M.W.L., 2007. Reproducibility of changes in behaviour and fMRI activation associated with sleep deprivation in a working memory task. Sleep 30, 61–70.

Locke, H.S., Braver, T.S., 2008. Motivational influences on cognitive control: behavior, brain activation, and individual differences. Cogn. Affect. Behav. Neurosci. 8, 99–112.

Lowe, C.J., Safati, A., Hall, P.A., 2017. The neurocognitive consequences of sleep restriction: a meta-analytic review. Neurosci. Biobehav. Rev. 80, 586–604.

Lowenstein, O., Loewenfeld, I.E., 1964. The sleep-waking cycle and pupillary activity. Ann. N. Y. Acad. Sci. 117, 142–156.

Ma, N., Dinges, D.F., Basner, M., Rao, H., 2015. How acute total sleep loss affects the attending brain: a meta-analysis of neuroimaging studies. Sleep 38, 233–240.

Makeig, S., Jung, T.P., Sejnowski, T.J., 2000. Awareness during drowsiness: dynamics and electrophysiological correlates. Can. J. Exp. Psychol. 54, 266–273.

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. Curr. Biol. 25, 1707–1716.

Massar, S.A.A., Libedinsky, C., Weiyan, C., Huettel, S.A., Chee, M.W.L., 2015. Separate and overlapping brain areas encode subjective value during delay and effort discounting. Neuroimage 120, 104–113.

Massar, S.A.A., Lim, J., Sasmita, K.S., Chee, M., 2016. Rewards boost sustained attention through higher effort: a value-based decision making approach. Biol. Psychol. 120, 21–27.

Massar, S.A.A., Csathó, Á., Van Der Linden, D., 2018. Quantifying the motivational effects of cognitive fatigue through effort-based decision making. Front. Psychol. 9, 843.

Massar, S.A.A., Lim, J., Sasmita, K., Chee, M.W.L., 2019. Sleep deprivation increases the costs of attentional effort: performance, preference and pupil size. Neuropsychologia 123, 169–177.

Menz, M.M., Büchel, C., Peters, J., 2012. Sleep deprivation is associated with attenuated parametric valuation and control signals in the midbrain during value-based decision making. J. Neurosci. 32, 6937–6946.

Meyniel, F., Sergent, C., Rigoux, L., Daunizeau, J., Pessiglione, M., 2013. Neurocomputational account of how the human brain decides when to have a break. Proc. Natl. Acad. Sci. U.S.A. 110, 2641–2646.

Mikulincer, M., Babkoff, H., Caspy, T., Sing, H., 1989. The effects of 72 hours of sleep loss on psychological variables. Br. J. Psychol. 80 (Pt. 2), 145–162.

Monk, T.H., 2012. Sleep and human performance. In: Morin, C.M., Espie, C.A. (Eds.), The Oxford Handbook of Sleep and Sleep Disorders. Oxford University Press, Oxford, pp. 1–23. I.C.M.M.C.a.E.E., (Pp. 1–23). Oxford.

Müller, T., Apps, M.A.J., 2019. Motivational fatigue: a neurocognitive framework for the impact of effortful exertion on subsequent motivation. Neuropsychologia 123, 141–151.

Mullin, B.C., Phillips, M.L., Siegle, G.J., Buysse, D.J., Forbes, E.E., Franzen, P.L., 2013. Sleep deprivation amplifies striatal activation to monetary reward. Psychol. Med. 43, 2215–2225.

Odle-Dusseau, H.N., Bradley, J.L., Pilcher, J.J., 2010. Subjective perceptions of the effects of sustained performance under sleep-deprivation conditions. Chronobiol. Int. 27, 318–333.

Ong, J.L., Asplund, C.L., Chia, T.T.Y., Chee, M.W.L., 2013. Now you hear me, now you don't: eyelid closures as an indicator of auditory task disengagement. Sleep 36, 1867–1874.

Parro, C., Dixon, M.L., Christoff, K., 2018. The neural basis of motivational influences on cognitive control. Hum. Brain Mapp. 39, 5097–5111.

Perogamvros, L., Dang-Vu, T.T., Desseilles, M., Schwartz, S., 2013. Sleep and dreaming are for important matters. Front. Psychol. 4, 474.

Pessiglione, M., Seymour, B., Flandin, G., Dolan, R.J., Frith, C.D., 2006. Dopamine-dependent prediction errors underpin reward-seeking behaviour in humans. Nature 442, 1042–1045.

Pessiglione, M., Vinckier, F., Bouret, S., Daunizeau, J., Le Bouc, R., 2017. Why not try harder? Computational approach to motivation deficits in neuro-psychiatric diseases. Brain 141, 629–650.

Pilcher, J.J., Huffcutt, A.I., 1996. Effects of sleep deprivation on performance: a meta-analysis. Sleep 19, 318–326.

Pilcher, J.J., Walters, A.S., 1997. How sleep deprivation affects psychological variables related to college students' cognitive performance. J. Am. Coll. Health 46, 121–126.

Pine, A., Seymour, B., Roiser, J.P., Bossaerts, P., Friston, K.J., Curran, H.V., Dolan, R.J., 2009. Encoding of marginal utility across time in the human brain. J. Neurosci. 29, 9575–9581.

Platt, M.L., Plassmann, H., 2014. Multistage valuation signals and common neural currencies. In: Glimcher, P.W., Fehr, E. (Eds.), Neuroeconomics: Decision Making and the Brain, second ed. Academic Press, London, pp. 237–258.

Poh, J.-H., Chee, M.W.L., 2017. Degradation of cortical representations during encoding following sleep deprivation. Neuroimage 153, 131–138.

Prevost, C., Pessiglione, M., Metereau, E., Clery-Melin, M.-L., Dreher, J.-C., 2010. Separate valuation subsystems for delay and effort decision costs. J. Neurosci. 30, 14080–14090.

Richter, M., Gendolla, G.H.E., 2009. The heart contracts to reward: monetary incentives and preejection period. Psychophysiology 46, 451–457.

Sanders, A.F., 1983. Towards a model of stress and human performance. Acta Psychol. (Amst) 53, 61–97.

Schmidt, L., Lebreton, M., Clery-Melin, M.-L., Daunizeau, J., Pessiglione, M., 2012. Neural mechanisms underlying motivation of mental versus physical effort. PLoS Biol. 10, e1001266.

Schonberg, T., Daw, N.D., Joel, D., O'doherty, J.P., 2007. Reinforcement learning signals in the human striatum distinguish learners from nonlearners during reward-based decision making. J. Neurosci. 27, 12860–12867.

Seaman, K.L., Brooks, N., Karrer, T.M., Castrellon, J.J., Perkins, S.F., Dang, L.C., Hsu, M., Zald, D.H., Samanez-Larkin, G.R., 2018. Subjective value representations during effort, probability and time discounting across adulthood. Soc. Cogn. Affect. Neurosci. 13, 449–459.

Shenhav, A., Botvinick, M.M., Cohen, J.D., 2013. The expected value of control: an integrative theory of anterior cingulate cortex function. Neuron 79, 217–240.

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. Annu. Rev. Neurosci. 40, 99–124.

Shingledecker, C.A., Holding, D.H., 1974. Risk and effort measures of fatigue. J. Mot. Behav. 6, 17–25.

Smith, D.V., Hayden, B.Y., Truong, T.K., Song, A.W., Platt, M.L., Huettel, S.A., 2010. Distinct value signals in anterior and posterior ventromedial prefrontal cortex. J. Neurosci. 30, 2490–2495.

Te Lindert, B.H.W., Itzhacki, J., Van Der Meijden, W.P., Kringelbach, M.L., Mendoza, J., Van Someren, E.J.W., 2018. Bright environmental light ameliorates deficient subjective 'liking' in insomnia: an experience sampling study. Sleep 41, zsy022.

Thomas, M., Sing, H., Belenky, G., Holcomb, H., Mayberg, H., Dannals, R., Jr, H.W., Thorne, D., Popp, K., Rowland, L., Welsh, A., Balwinski, S., Redmond, D., 2000. Neural basis of alertness and cognitive performance impairments during sleepiness. I. Effects of 24 h of sleep deprivation on waking human regional brain activity. J. Sleep Res. 9, 335–352.

Venkatraman, V., Chuah, Y.M.L., Huettel, S.A., Chee, M.W.L., 2007. Sleep deprivation elevates expectation of gains and attenuates response to losses following risky decisions. Sleep 30, 603–609.

Venkatraman, V., Huettel, S.A., Chuah, L.Y.M., Payne, J.W., Chee, M.W.L., 2011. Sleep deprivation biases the neural mechanisms underlying economic preferences. J. Neurosci. 31, 3712–3718.

Verguts, T., Vassena, E., Silvetti, M., 2015. Adaptive effort investment in cognitive and physical tasks: a neurocomputational model. Front. Behav. Neurosci. 9, 57.

Vyazovskiy, V.V., Olcese, U., Hanlon, E.C., Nir, Y., Cirelli, C., Tononi, G., 2011. Local sleep in awake rats. Nature 472, 443–447.

Wagner, D.T., Barnes, C.M., Lim, V.K.G., Ferris, D.L., 2012. Lost sleep and cyberloafing: evidence from the laboratory and a daylight saving time quasi-experiment. J. Appl. Psychol. 97, 1068–1076.

Westbrook, A., Braver, T.S., 2015. Cognitive effort: a neuroeconomic approach. Cogn. Affect. Behav. Neurosci. 15, 395–415.

Wilhelm, B., Wilhelm, H., Lüdtke, H., Streicher, P., Adler, M., 1998. Pupillographic assessment of sleepiness in sleep-deprived healthy subjects. Sleep 21, 258–265.

Wilkinson, R.T., 1961. Interaction of lack of sleep with knowledge of results, repeated testing, and individual differences. J. Exp. Psychol. 62, 263–271.

Zenon, A., Sidibe, M., Olivier, E., 2014. Pupil size variations correlate with physical effort perception. Front. Behav. Neurosci. 8, 286.

Zenon, A., Solopchuk, O., Pezzulo, G., 2019. An information-theoretic perspective on the costs of cognition. Neuropsychologia 123, 5–18.