

Title:

Neurobehavioral Correlates of How Time-on-task and Sleep Deprivation Modulate
Deployment of Cognitive Effort

Stijn A.A. Massar¹, Julian Lim¹, Karen Sasmita^{1,2}, Bindiya L. Ragunath^{1,3}, & Michael W.L.
Chee^{1*}

¹ Centre for Sleep and Cognition, Yong Loo Lin School of Medicine, National University of
Singapore

² Department of Psychology, Cornell University, Ithaca, NY, USA

³ Division of Psychology, Nanyang Technological University, Singapore

* Corresponding author: Michael W.L. Chee

Centre for Sleep and Cognition
Yong Loo Lin School of Medicine
National University of Singapore

Email: michael.chee@nus.edu.sg

Phone: +65 65164916

Abstract

Sustaining attention is highly demanding and can falter if there is a shift in willingness to exert effort. Motivated attentional performance and effort preference were tracked in relation to increasing time-on-task (Experiment 1) and sleep deprivation (Experiment 2). Performance decrement with time-on-task was attenuated with reward, while preference to deploy effort decreased with longer task duration. Sleep deprivation, accentuated performance decline with time-on-task, and was accompanied by greater effort-discounting. Motivated attention performance was associated with higher fronto-parietal activation, in both normal and sleep deprived conditions. However, after sleep deprivation modulation of activation by reward was reduced in the anterior cingulate cortex (ACC) and left anterior insula (aIns). Together, these results depict how motivational decline affects performance when one gets tired after sustained task performance and/or sleep deprivation.

Keywords: Attention, Motivation, Reward, Decision-Making, Time-on-Task, Sleep Deprivation

Introduction

Prolonged performance of an attention demanding task results in slowing of responses and increased errors (Warm, Parasuraman, Matthews 2008) and constitute time-on-task effects. Accompanying these behavioral alterations is reduced fronto-parietal activation (Coull et al., 1998, Warm and Parasuraman, 2007, Langner and Eickhoff, 2013, Lim et al., 2010) that reflects decline in top-down attentional control. Resource theories of fatigue posit these that these phenomena arise because prolonged task performance depletes finite neural resources.

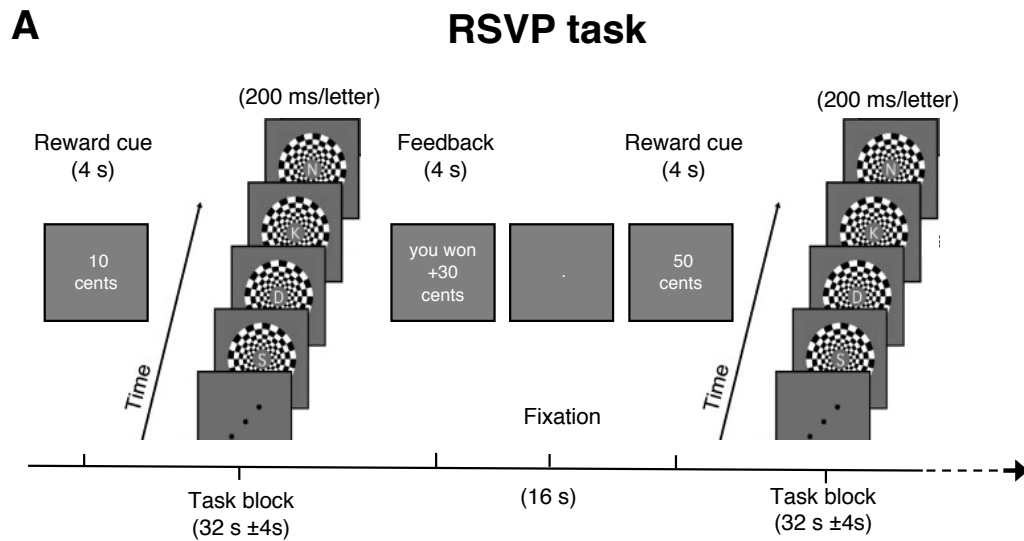
Sustained attention is highly sensitive to sleep deprivation (SD) (Lim and Dinges, 2008). Moreover, time-on-task effects can be exacerbated after SD (Van Dongen et al., 2011). Performance deficit in SD arises from state specific mechanisms such as the stochastic drop-out of neural activity in cortical columns arising from ‘local sleep’ (Vyazovskiy et al., 2011) or changes in brain connectivity (Yeo et al., 2015, Wang et al., 2016). However, in common with time-on-task effects, SD is also accompanied reduced activation in fronto-parietal brain networks (Chee and Tan, 2010, Chee et al., 2008, Lim et al., 2007, for a review see Ma et al., 2015). Indeed, brain regions showing reduced activation with time-on-task and SD show significant overlap (Asplund and Chee, 2013).

While resource depletion accounts remain the most common explanation for the observed effects of time-on-task and SD, it has recently been argued that both conditions are accompanied by a loss in motivation to exert appropriate effort (Massar et al., 2019a, Müller and Apps, 2019). Underlying both observations is the theory that the brain continuously compares energetic costs against expected rewards (or benefits), especially when one is tired (Boksem and Tops, 2008). If task costs outweigh the benefits, an individual may decide to withdraw effort and reduce standards of task performance (Hockey, 2013, Kanfer and Ackerman, 1989). Such a shift in effort preference may contribute to the observed reductions in brain activation and performance (Massar et al., 2018, Müller and Apps, 2019).

This cost-benefit analysis is thought to be undertaken by the anterior insula (aIns), dorsolateral Prefrontal Cortex and dorsal portion of the medial prefrontal cortex (dmPFC; Boksem and Tops, 2008, Müller and Apps, 2019). The anterior insula has been advanced as an important hub for evaluating task performance. It processes interoceptive information about the internal state of the organism (Craig, 2009), encodes the subjective perception of effort (Otto et al., 2014), and signals if it is appropriate to cease effortful action (Meyniel et

al., 2013). Complementing these functions, the dorsal medial prefrontal cortex (dmPFC), including the anterior cingulate cortex (ACC) integrate information about expected rewards and effort costs (Klein-Flügge et al., 2016, Prevost et al., 2010, Shenhav et al., 2013, Vassena et al., 2017). Moreover, the ACC may direct motor and cognitive areas to prioritize high value processes. The lateral Prefrontal cortex tracks subjective cognitive effort, biasing action away from high effort task options (McGuire and Botvinick, 2010). Together, these brain areas are thought to implement the proposed decision process by integrating cost and benefit information given the internal state, computing subjective values of actions, and then energizing the action chosen on the basis of its highest subjective value (Chong et al., 2016, Pessiglione et al., 2017).

In this study we examined the motivational account of performance decrement under two related yet distinct contexts where it is expected to operate i.e. time-on-task (Experiment 1) and sleep deprivation (Experiment 2). Participants underwent fMRI while performing an effortful attentional task under different reward conditions (Figure 1A). Changes in performance and brain activation were tracked for the different incentive levels. To examine the underlying basis for motivated behavior, participants performed an out-of-scanner value-based decision task (discounting task; Figure 1B), in which they pitted the value of potential rewards against the costs of performing the attention task for a specified duration. We showed that attentional performance deteriorated with time-on-task, and that this effect was less pronounced under the high incentive condition. In the decision task, participants discounted the value of available rewards when longer task performance was required. Moreover, both deterioration of attentional performance and value discounting were accentuated after sleep deprivation. Lastly, improved performance with higher reward was associated with greater activation of attention-related brain areas including the aIns, and ACC/dmPFC. Conversely, activity in these areas was reduced with time-on-task and sleep deprivation.



B **Discounting task**

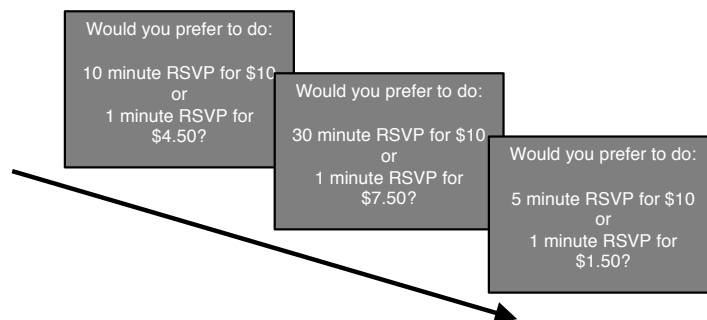


Figure 1. Schematic of experimental tasks, with (A) the rapid serial visual processing (RSVP) task. Letter streams (200ms/letter) are presented in 32 sec (\pm 4sec) task blocks. Participants had to detect “J” or “K” target letters and respond with a left or right button press, respectively. Each correct target detection was rewarded. Task blocks were preceded by a reward cue, that indicated the incentive level for correct detections in that block (0, 10, or 50 cent). Reward feedback was given after each block. Each task run consisted of six task blocks. A total of six task runs were performed. (B) Example choice trials in the discounting task, in which further performance of the RSVP task (1 to 30 minutes) was weighed against available reward (\$0 to \$10). After completion of the discounting task, one choice trial was randomly drawn for execution.

Results

Motivated Attention Performance

Participants performed six runs of a rapid serial visual processing task (RSVP). Each run consisted of six task blocks during which participants viewed a rapid stream of letter stimuli. Participants had to detect the target letters “J” and “K” and responded by pressing a left or right button, respectively. Each block was preceded by a reward cue that signaled the level of reward (low = 0 cent, medium = 10 cents or high = 50 cents) that could be earned for correct and fast target responses.

Experiment 1. Detection accuracy for the RSVP task (Fig. 2A) was analyzed using a repeated measures ANOVA with Reward (low, medium, high), and Time-on-task (run: 1, 2, 3, 4, 5, 6) as within-subject factors. There was a significant main effect of Reward ($F(2, 46) = 5.98, p = .015, \eta_p^2 = .206$), but no main effect of Time-on-task ($F(5, 115) = .955, p = .45$) or Reward x Time-on-task interaction ($F(10, 230) = 1.77, p = .068, \eta_p^2 = .071$). However, a linear interaction contrast (taking into account the first and last runs) was significant ($F(1, 23) = 5.017, p = .035, \eta_p^2 = .179$). Planned t-tests showed that the time-on-task decrement was significant only in low reward task blocks ($t(23) = 2.06, p = .05$), but not for task blocks with medium or high rewards (medium: $t(23) = -.49, p = .64$; high: $t(23) = -1.16, p = .26$).

Experiment 2. Participants performed the same motivated RSVP task once after a night of normal sleep (Rested Wakefulness: RW), and once after a night of total sleep deprivation (SD). Accuracy data for Experiment 2 are displayed in Fig. 2D. Analysis of the RW session mostly replicated results from Experiment 1. There was a significant main effect of Reward ($F(2, 50) = 8.71, p = .002, \eta_p^2 = .258$), but no main effect of time-on-task or interaction. This time, the linear interaction contrast was not significant ($F(1, 25) = 3.565, p = .071, \eta_p^2 = .125$).

To examine the changes in accuracy under SD, a State (RW, SD) x Reward (low, medium, high) x Time-on-task (run: 1, 2, 3, 4, 5, 6) repeated measures ANOVA was performed. There were significant main effects of State ($F(1, 25) = 47.21, p < .001, \eta_p^2 = .654$), Reward ($F(2, 50) = 16.05, p < .001, \eta_p^2 = .391$) and Time-on-task ($F(5, 125) = 5.341, p < .001, \eta_p^2 = .186$) as well as a significant State x Time-on-task interaction ($F(5, 125) = 3.059, p = .012, \eta_p^2 = .109$), indicating that overall the time-on-task decrement was more pronounced in SD than RW. All other interaction effects were non-significant (all F 's < 1.02).

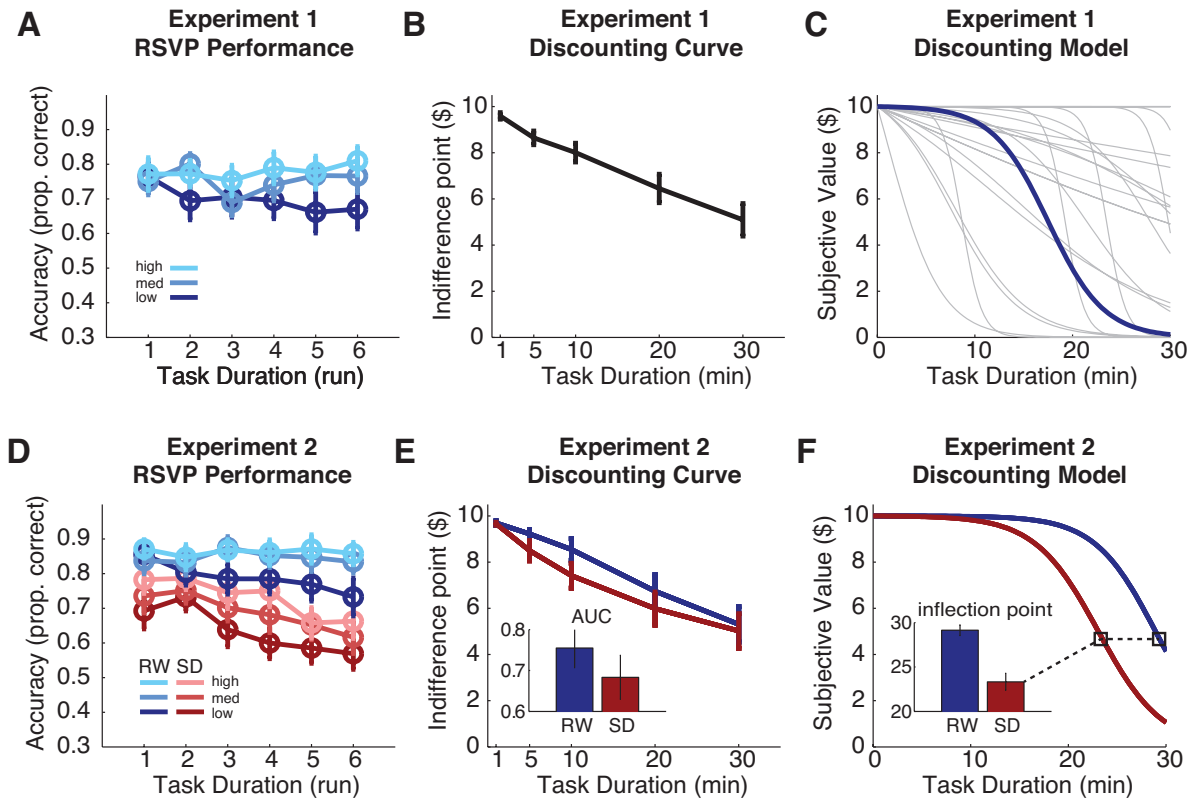


Figure 2. Behavioral results for Experiment 1 (upper panels), and Experiment 2 (lower panels) showing performance on RSVP task at different levels of reward (A & D), Model-free analysis of choice preference in the Discounting task (B & E: with inset in panel E showing area under the curve [AUC]), and computational model fit of the Discounting task (C: light grey lines show individual fits; F: inset shows inflection point of discounting model [p-parameter]). RW = Rested Wakefulness, SD = Sleep Deprivation.

Discounting Task

Following completion of the RSVP task, participants performed a value-based decision task in which they were offered monetary rewards for performing the RSVP task for an extended duration (1 to 30 minutes). On each trial of the discounting task participants were presented with a choice between performing the RSVP for a short duration to receive a small reward (<\$10), or performing the RSVP for a longer duration to receive a larger reward (\$10). Participants had to indicate their preference on each trial. Reward values were systematically updated to approach the participant's individual indifference point, reflecting the discounted reward value that the participant considered equally attractive as \$10 at a longer task duration (subjective value).

Experiment 1. Analysis of the discounting curve showed that reward value was significantly discounted with longer task duration ($F(1, 23) = 44.91, p < .001, \eta_p^2 = .661$; Fig2B). While the value of a \$10 reward was discounted slightly when a 5-minute RSVP was required (mean indifference point = \$8.64 (1.46)), it was discounted more strongly when 30 minutes of RSVP performance were required (mean indifference point = 5.09 (3.45)). Computational modeling (see Methods) of the choice data indicated that the Sigmoid discounting model (Fig 2C) fit the data better than other models (Hyperbolic or Exponential). This concurs with recent findings concerning effort-based decision making (Klein-Flügge et al., 2015, Massar et al., 2019b). The sigmoid discounting model is characterized by three free parameters, 1) an inflection point (p -parameter; indicating the task duration at which the offered reward is discounted to half its original value), 2) a slope (k -parameter; indicating the steepness of discounting around the inflection point), and 3) an inverse temperature parameter (Softmax β parameter), indicating how strongly choices were determined by the given value function (inverse randomness).

Experiment 2. In Experiment 2 reward value was similarly discounted with longer task durations (Duration main-effect: $F(4, 100) = 26.98, p < .001, \eta_p^2 = .519$). Further there was a significant State main-effect ($F(1, 25) = 5.44, p = .028, \eta_p^2 = .179$), showing that reward value was more heavily discounted under SD compared to RW. The state effect was further examined through two additional methods. First, we extracted the area under the discounting curve (AUC), which is a model-free measure of discounting (Myerson et al., 2001). A paired t-test showed that the AUC was significantly lower in SD compared to RW ($t(25) = 2.32, p = .029$, Cohen's $d = .455$; Fig. 2E inset). Secondly, we fitted a computational model to the individual choice data. Comparison of the individual model parameters between SD and RW showed that the Sigmoid slope (k -parameter) was not altered between SD and RW ($t(25) = 1.33, p = .195$). However, there was a significant shift in the inflection point (p -parameter), such that in SD compared to RW, shorter durations of required task performance led to discounting of a reward to half its original value ($t(25) = 2.09, p = .047$, Cohen's $d = .41$; Figure 2F). Furthermore, choice randomness was higher (i.e. Softmax β parameter was lower) in the SD session compared to the RW session ($t(25) = 2.204, p = .037$, Cohen's $d = .43$).

1 *Imaging results*

2 To examine BOLD activation during performance of the motivated RSVP task,
3 a general linear model (GLM) analysis was performed, including a regressor modeling the
4 overall activation during task blocks. An additional Reward regressor modeled the parametric
5 modulation of task activation with reward level (indicating increasing activation during
6 higher reward blocks).

7 *Experiment 1.* Analysis of the main task regressor (Fig 3A) showed large clusters of
8 activation in bilateral occipital cortex, as well as activation in attention related areas
9 comprising prefrontal clusters in the bilateral inferior frontal gyrus stretching to the anterior
10 insula (aIns), bilateral superior frontal gyrus stretching to the cingulate gyrus, and lateral
11 prefrontal clusters comprising the left precentral and middle frontal gyrus, and right inferior
12 frontal gyrus, and parietal clusters in the right precuneus and left superior parietal lobule.
13 Further, both caudate nuclei were activated.

14 *Reward modulation:* Activation in areas engaged during task performance increased
15 with incentive value. Moreover, clusters that were modulated by reward extended medially
16 into the anterior cingulate cortex (ACC), and laterally into the superior and middle frontal
17 gyrus, mainly right lateralized. Parietal activation was also modulated by reward, involving
18 the inferior parietal lobule bilaterally. Several additional areas showed reward modulation
19 including clusters in the ventral striatum, thalamus and cerebellum.

20 *Time-on-Task:* To examine changes in activation over time-on-task, a second GLM
21 analysis was performed, modeling task activation in the six task runs separately (with
22 separate regressors for each reward level, in each run). Systematic changes in activation over
23 time (indicated by a significant run main effect) were found in visual areas, and in the medial
24 frontal gyrus/cingulate cortex, middle frontal gyrus, and precuneus (Figure 4A). Despite
25 activation declining over time-on-task in all three reward conditions, high reward trials
26 continued to show greater activation than low reward trials over time (Figure 4B).

Experiment 1

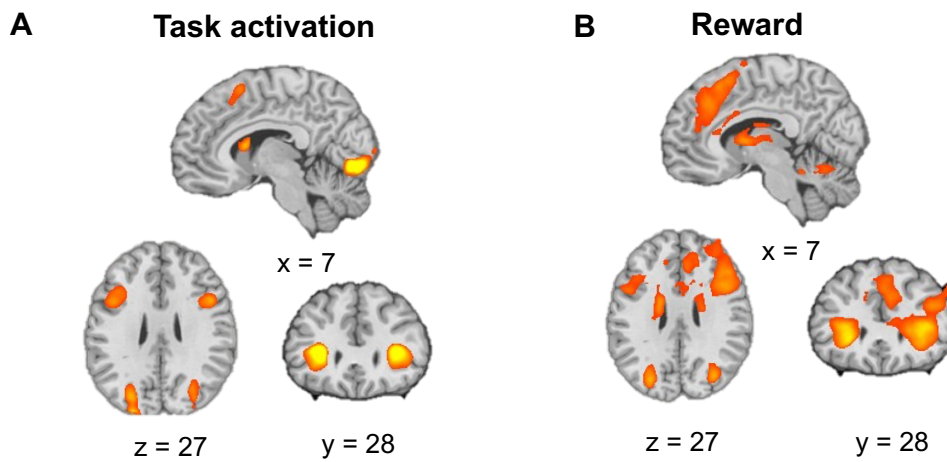


Figure 3. Activation during the RSVP task in Experiment 1. A) main effect of task, B) parametric modulation of activation by reward.

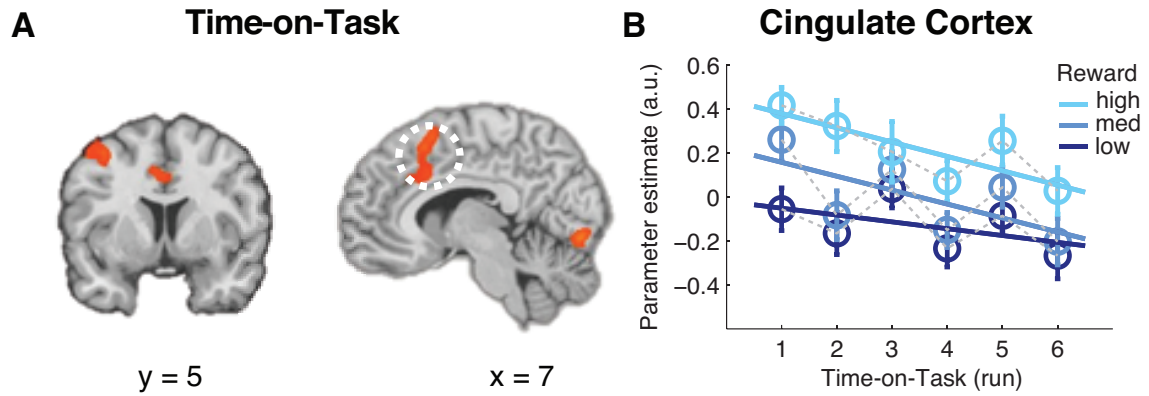


Figure 4. A) Time-on-Task effect in task activation, B) time course of task activation in dmPFC/ACC.

Experiment 2. The main effect of task seen in Experiment 1 was also present in both the RW and SD sessions of Experiment 2 with activation of visual cortex, and fronto-parietal areas (Fig 5A). In RW, activation in the attention-related areas was up-regulated in higher reward blocks with extension to additional areas of cingulate cortex, striatum and the thalamus (Fig 5B). In SD this reward modulation appeared in similar brain regions, but was weaker (Fig 5B). Direct contrast of the reward modulation during RW versus SD yielded two clusters, a significant cluster in the left anterior insula and a small patch of medial frontal gyrus, that did not survive cluster level correction (see Fig 6).

Experiment 2

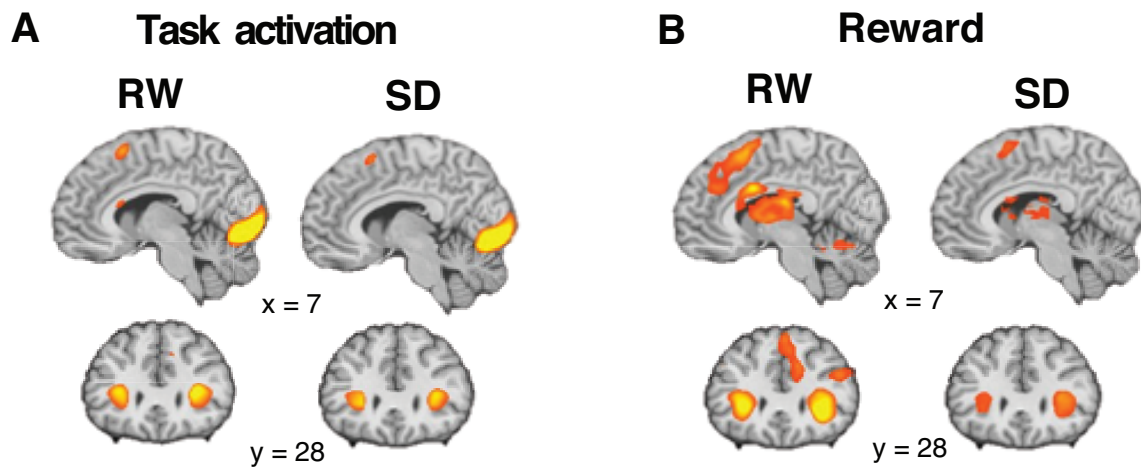


Figure 5. A) Task activation in Experiment 2 during Rested Wakefulness (RW) and Sleep Deprivation (SD). B) Parametric modulation by reward in RW and SD.

Reward RW > SD

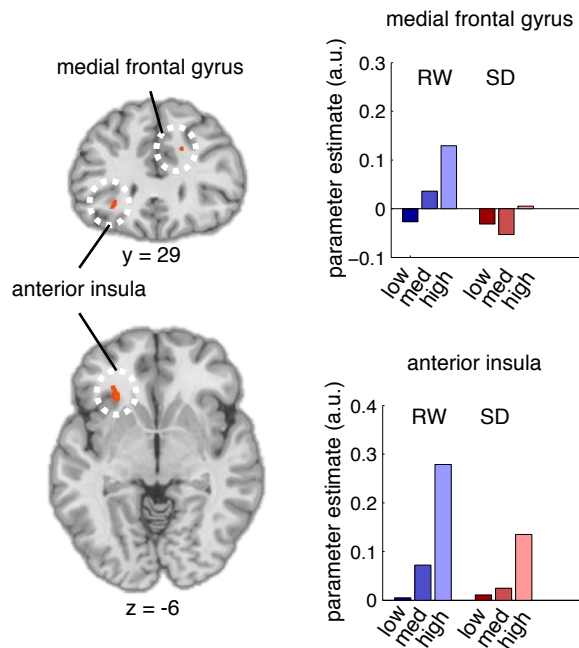


Figure 6. Areas showing reduction in reward modulation during SD compared to RW with, medial prefrontal cortex (upper panels), and left anterior insula (lower panels). Bar graphs show task activation in the indicated medial frontal gyrus and anterior insula clusters, modeled for each reward condition.

Discussion

We studied the effects of motivation, time-on-task and sleep deprivation on task performance as well as their interactions. We also measured discounting behavior, and brain activation associated with task performance under different conditions. In addition to replicating previous findings that task duration and sleep deprivation negatively impact the behavioral and neural correlates of motivated behavior, we found that: 1) Performance was influenced by reward motivation and by sleep deprivation, 2) Reward value was discounted with longer task durations and with SD, 3) Brain activation in areas mediating attentional control was lowered with time-on-task but tempered by reward particularly during SD. Overall, these data underscore the interaction between effortful task performance and motivation, and support a motivational account of fatigue and its modulation by sleep deprivation.

Performance decrement is modulated by motivation

Deterioration of attentional performance over time is one of the most robust behavioral hallmarks of prolonged task performance (for reviews see Langner and Eickhoff, 2013, Warm et al., 2008). The time-on-task decrement is often magnified by task load as well as by sleep deprivation (Lim and Dinges, 2008). This is commonly taken to reflect that the participant is no longer able to muster the energetic resources to maintain performance. Results from the current study show that performance declines over time can be mitigated by the provision of incentives. In conditions of normal sleep (Exp1 & Exp2 RW), performance only deteriorated in the low reward blocks, while high detection accuracy was maintained throughout in the higher reward blocks. This is in line with the idea that when fatigued, resources can still be directed to facilitate task performance if the reward for maintaining performance is sufficiently high. Several earlier studies have shown similar reward modulation of time-on-task effects on shorter time scales (i.e. ~10 minutes; Esterman et al., 2016, Massar et al., 2016). Other studies have shown that, even after sustained task performance for 90 minutes or longer, performance can be boosted if incentives for performing well are provided (Boksem et al., 2006, Hopstaken et al., 2014, but see Gergelyfi et al., 2015).

As expected, performance was impaired with sleep deprivation compared to rested wakefulness in Experiment 2. Furthermore, time-on-task related performance decline was steeper during SD. While reward motivation modulated performance at all points in time, it

1 did not interact with the time-on-task effects in SD. Although this only partially replicated
2 results from an earlier study (Massar et al., 2019b), attention could still be substantially
3 improved by high reward during SD. Of note, the worst performance in the high reward
4 blocks (run 6) was at the level of low-reward performance in the first run (around 60%
5 accuracy).

6 7 *Reward value is discounted with task duration*

8 The discounting task provided further insight into the proposed decision processes that may
9 underlie the withdrawal of attentional effort with longer task duration. Participants were
10 given the free choice between performing the attention task for an additional short period of
11 time (1 minute) and receiving a smaller reward, or performing the task for a specified longer
12 duration (up to 30 minutes) for a higher reward. When longer task durations were required,
13 participants often opted to forego the higher reward by choosing a shorter task.

14 These findings demonstrate that task performance is considered as a cost by which
15 reward value is discounted (Westbrook and Braver, 2015). Choice behavior best fit a sigmoid
16 discounting function where with small increases in effort, reward value is minimally
17 discounted, while with larger increases in effort, discounting becomes steeper (i.e. the
18 discounting function is initially concave). Similar discounting functions were found when
19 effort was manipulated along a dimension other than task duration (e.g. cognitive task
20 difficulty or physical exertion; Chong et al., 2017, Klein-Flügge et al., 2016, Klein-Flügge et
21 al., 2015, Białaszek et al., 2017). Importantly, discounting was more pronounced after sleep
22 deprivation, paralleling the finding that performance decline with time-on-task in the RSVP
23 task was exacerbated during SD. The observation that task duration had a stronger influence
24 on preference in SD than in RW concurs with the finding that effort discounting also
25 increases after SD (Libedinsky et al., 2013, Massar et al., 2019b) and suggests a loss in
26 motivation to perform.

27 28 *Motivated performance is supported by a cingulate-insula network*

29 A third finding from the current study was that reward modulates activation of brain areas
30 involved in top-down control of attention. A network of frontal (aIns, dmPFC, lateral PFC)
31 and parietal areas (precuneus/IPL) that was involved in overall task performance, was
32 modulated by incentive value. Under normal sleep conditions (Exp1 & Exp2 RW) reward
33 modulated activation extended into the ACC, and lateral middle and superior frontal gyrus,

1 and into clusters in the thalamus and striatum. With time-on-task, activation in the
2 ACC/dmPFC, middle frontal gyrus and precuneus decreased. These areas closely match the
3 regions found in a previous fMRI study (Asplund and Chee, 2013). The modulation of aIns
4 activation by reward decreased following SD.

5 The insula, ACC/dmPFC and lateral frontal cortex are thought to be key nodes in a
6 network integrating reward value and effort costs (Vassena et al., 2017), and coordinating the
7 allocation of effort to courses of action with the highest net gain (Pessiglione et al., 2017). In
8 several meta-analyses, these areas show remarkable overlap in their response to reward for
9 task performance (Parro et al., 2018), time-on-task (Langner and Eickhoff, 2013), and sleep
10 deprivation (Ma et al., 2015, for a comparison of overlap see Massar et al., 2019a). As such
11 this network may serve to redirect neural resources when effort is perceived to outweigh
12 rewards when one is tired (Müller and Apps, 2019), or in our case, sleep deprived.

13 These areas have repeatedly featured in effort-based decision making tasks- involving
14 exertion of physical force (Bonnelle et al., 2016, Burke et al., 2013, Klein-Flügge et al., 2016,
15 Prevost et al., 2010), and cognitive effort (Chong et al., 2017, Massar et al., 2015). Activation
16 in the ACC during effort-based decision making is correlated with individual differences in
17 self-reported persistence (Kurniawan et al., 2010). Interestingly, electrical or magnetic
18 stimulation of the medial frontal cortex can induce a sense of motivation (Parvizi et al.,
19 2013), and bias choices to higher effort options (Zenon et al., 2015). The current data add to
20 these findings that both time-on-task and sleep deprivation reduce activation in this network,
21 potentially reflecting the reduced motivation to exert effortful control.

22 23 *Conclusion*

24
25 In summary, the current study shows that motivation and attention interact through a fronto-
26 parietal brain network. With increasing time-on-task and sleep deprivation, performance and
27 willingness to exert effort deteriorate. This is accompanied by reduced activation in the ACC
28 and the aIns, suggesting a key-role for these areas in integrating the costs and benefits of
29 cognitively effortful performance, and the modulation of how these costs and benefits are
30 perceived when we get tired.

1 **Methods**

3 *Participants & Procedure*

4 *Experiment 1:* Twenty-four participants were recruited from the student population of the
5 National University of Singapore (10 females, mean age (stdev.) = 22.7 years (2.26)). All
6 participants were right-handed, had no contra-indications for MRI scanning, and had no
7 history of psychiatric or neurological disorders. The protocol was approved by the
8 Institutional review board of the National University Singapore, and all participants provided
9 informed consent prior to testing. Participants came to the lab for one session, during which
10 they were scanned while performing a motivated attention task. This was followed by an out-
11 of-scanner value-based decision-making task (Discounting). This session lasted
12 approximately 1.5 hours. Participants were paid \$25 for their time, plus a performance-
13 dependent bonus of up to \$25.

14 *Experiment 2:* An independent sample of 28 participants was recruited for a sleep
15 deprivation experiment (15 females, mean age (stdev.) = 22.9 years (3.28)). The same
16 inclusion criteria as for Experiment 1 were applied, with additional criteria that participants
17 should have regular sleeping habits, no symptoms or history of sleep disorders, and should
18 not work irregular or night shifts. Participants in Experiment 2 were studied in two sessions.
19 During the Rested Wakefulness (RW) session they slept in the lab (bedtime 11pm to 7am).
20 They were then woken up and the experimental session started at 8am. In the Sleep
21 Deprivation (SD) session participants were kept awake overnight, supervised by a research
22 assistant. They were allowed to engage in non-strenuous activities. In the morning, the testing
23 session commenced at 6am. This is when cognition is usually most strongly affected by the
24 combination of the circadian factors and the effects of extended wakefulness. In both the RW
25 and SD sessions testing procedures were the same as in Experiment 1. Participants performed
26 a motivated attention task, and a Discounting task. Participants received \$80 for completion
27 of both sessions, plus a performance-dependent bonus of up to \$25 per session.

29 *Motivated Attention Task*

30 Participants performed an attention-demanding task (Asplund and Chee, 2013) while in the
31 scanner. A rapid serial visual presentation (RSVP) stream of white letters was presented on a
32 grey background, surrounded by a flickering checkerboard (10 Hz). Letters were presented
33 for 200 ms each, in direct succession. Participants were required to press one of two target

buttons whenever they detected a “J” or a “K” letter in the RSVP stream. Task blocks lasted for 32 ± 4 seconds. Each task block contained 5 to 7 target letters separated by at 2 to 10-seconds inter target interval. Critically, each task block was preceded by reward cue (1c, 10c, or 50c), that informed participants of the incentive that could be earned for correct and fast target responses during that block. An RT cut-off was determined based on the median RT of an out-of-scanner practice run. A task run lasted for 6.5 minutes and comprised 6 task blocks (2 blocks per incentive level in counterbalanced order). Participants performed a total of 6 task runs. The main performance metric was target detection accuracy, which was quantified per run for each incentive level separately. Prior to scanning, participants performed a practice run outside the scanner.

Discounting Task

After completion of the motivated RSVP Task, participants performed an out-of-scanner Discounting Task. In this task participants were to decide how they would spend the last 30 minutes of the experimental session, indicating their preference between performing the RSVP task for another duration of time, given a specified reward. Participants were presented with a series of choice trials. On each trial they could choose to perform a short version of the RSVP task (1 minute) and receive a low reward, or a longer version of the RSVP task (5, 10, 20, or 30 minutes) to receive a higher reward. The higher reward for the longer duration task was always \$10. The lower reward was systematically varied from trial to trial using an adaptive staircase method. If the participant chose to do the longer task, the lower reward for the shorter task was adjusted upwards in the next trial. If the participant chose to do the shorter task, the reward amount for the shorter task was adjusted downwards for the next trial. This procedure allowed the estimation of the lower amount of money an individual considered equally valuable as the higher amount \$10 at a given task duration (indifference point). A discounting curve was constructed by plotting the indifference points at all different task durations, from which the area under the curve (AUC) was calculated as a model-free summary metric of the individual’s extent of discounting (larger AUC indicates less discounting). To make choices incentive compatible, one choice trial was drawn at random for execution after all choices were made. Participants had to perform the RSVP task for the duration of the chosen option on that trial, before receiving the associated reward. To ensure that decisions were not made on the basis of the delay to reward receipt (delay discounting), all participants had to stay in the lab for a fixed duration of 30 minutes.

Model-based analysis: To more formally characterize the shape of the discounting curve, we fitted a sigmoid function previously found to describe effort-based choice well (Klein-Flügge et al., 2016, Klein-Flügge et al., 2015, Massar et al., 2019b). This model predicts that a reward is discounted by small amounts when only a short duration of task performance is required. At longer task durations, discounting becomes steeper and eventually plateaus to approach zero at very long durations of task performance (see Fig7 A&B).

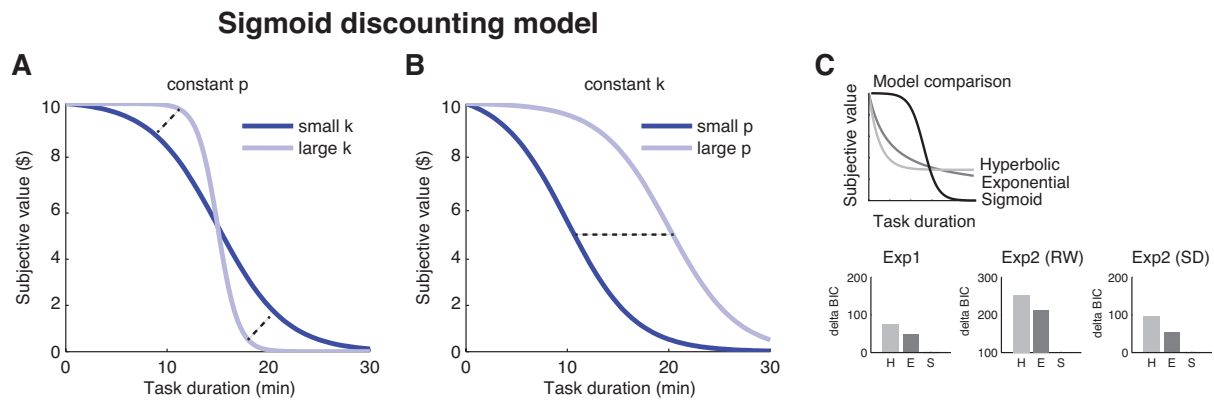


Figure 7. Illustration of the sigmoid discounting model with (A) different values of k (given constant p), (B) different values of p (given constant k), and (C) comparison of model fit against hyperbolic and exponential models. BIC = Bayesian Information Criterion, H = Hyperbolic, E = Exponential, S = Sigmoid.

This model can be formalized by the following equation:

$$SV_{long} = R * \left(1 - \left(\frac{1}{(1 + e^{-k*(T-p)})} - \frac{1}{(1 + e^{k*p})} \right) \cdot \left(1 + \frac{1}{(1 + e^{k*p})} \right) \right)$$

Where SV_{long} is the subjective value of a reward R at task duration T . The model has two free parameters that are fitted to individual choice behavior. The parameter k indicates the slope of the discounting function, while p indicates the inflection point (time point at which the reward is discounted to half its original value). Choice probability for each trial was modeled following a Softmax function:

$$P(\text{choose long}) = \frac{1}{(1 + e^{-\beta*(SV_{long} - V_{short})})}$$

Where P is the probability of choosing the longer task. The free parameter β denotes the inverse choice randomness (inverse temperature), indicating how strongly choices follow the given value function (i.e. the influence of value difference between the subjective value of the longer task option SV_{long} , and the value of the shorter duration option V_{short}). Individual participants' choice data were fitted using the fmincon algorithm in Matlab (MathWorks, Natick, MA) to find free parameter values that optimized the model fit (minimize negative log likelihood). To test whether the sigmoid model described choice data well, model fit was compared to more traditional hyperbolic and exponential discounting models using the Bayesian information criterion (BIC; Schwartz, 1978). A smaller BIC indicates better model fit (Fig7 C, where delta BIC indicates the difference score with regard to the best fitting model). To compare model parameters between the RW and SD session in Experiment 2, paired-samples t-tests were performed for the sigmoid p , k , β -parameters (square root transformed to correct for non-normality; Peters et al., 2012).

fMRI data acquisition & processing

Functional imaging during the Motivated Attention Task was conducted on a Siemens 3T Prisma scanner (Siemens, Erlangen, Germany). Functional runs were acquired using an interleaved echo-planar imaging (EPI) sequence (TR: 2000ms; TE: 30ms; flip angle: 90°; field-of-view: 192 × 192 mm; matrix size: 64 × 64). Thirty six 3-mm oblique axial slices were collected, aligned to the intercommissural plane. A T1-weighted high-resolution 3D-MPRAGE (1mm x 1mm x 1mm) sequence (TR: 2300 ms; TE: 2.28 ms; TI = 900 ms; flip angle = 8°; field-of-view: 256 x 240 mm; BW = 240 Hz/Px; matrix size: 256 x 240, voxel size: 1 mm³; 192 slices) was performed at the end of the functional runs. During functional imaging, an MRC 12M-I eye-tracking camera (MRC Systems GmbH, Germany) was used to monitor eye closure. Audio messages were delivered through an intercom if a participant closed their eyes for ≥10 seconds, to reduce episodes of sleep.

Preprocessing: Functional imaging data were slice-time corrected and motion corrected using rigid body translation and rotation parameters. Individual participants' anatomical scans were then reconstructed into surface representations and functional data were registered to structural images using the reconstructed cortical surfaces (Greve and Fischl, 2009, <http://surfer.nmr.mgh.harvard.edu/fswiki/FsFast>). The structural images were in turn nonlinearly registered to the MNI152 space (Buckner et al., 2011, Yeo et al., 2011). The resulting nonlinear deformations were used to warp the functional data into MNI152 space

1 and smoothed with a 6 mm FWHM smoothing kernel. The first four volumes of each scan
2 run were discarded to allow for signal saturation.

3 *Statistical analysis:* To analyze overall activation during task performance and the
4 modulation of activation by rewards a GLM analysis with two predictors of interest was
5 performed in BrainVoyager QX version 2.6.1.2318 (Brain Innovation, Maastricht, the
6 Netherlands). The first regressor modeled the overall activation during task performance by
7 modeling task blocks as boxcar functions with the length of the block duration. An additional
8 parametric regressor modeled the incentive level for each block, orthogonalized with respect
9 to the main task regressor ([-1 0 1] for low, medium and high reward). To analyze time-on-
10 task changes in activation, a second GLM with 18 predictors of interest was performed in
11 which task blocks for each reward condition (low, medium, high) were modeled for each task
12 run separately (run 1-6). Areas that showed a significant main effect of task run were further
13 examined to determine the direction of this effect. In all GLMs an additional regressor of
14 non-interest was included to model motor responses. 6 regressors were included to account
15 for head motion. All regressors were convolved with a hemodynamic response function and
16 GLMs were accordingly computed. Resulting statistical maps were thresholded at $p < .001$
17 (uncorrected), and corrected ($p < .05$) using an iterative cluster size thresholding algorithm
18 (Goebel et al., 2006). In Experiment 1, one participant had excessive head motion (> 1 mm
19 displacement in multiple runs), and was excluded from fMRI analysis (final $N = 23$). In
20 Experiment 2, two participants were excluded from analysis as they were unable to perform
21 the attentional task under SD (final $N = 27$). One participant completed only five runs of the
22 attention task, and was excluded from the time-on-task analysis (final $N = 26$). For another
23 participant data from the discounting task were not correctly saved in one session, and were
24 not included in the discounting analysis (final $N = 26$).

26 **Acknowledgments**

27 The authors would like to thank James Teng, Teck Boon Teo, and Ksenia Vinogradova for
28 technical assistance and help collecting data. This work was supported by grants awarded to
29 Dr. Michael Chee by the National Medical Research Council (NMRC/STaR/0015/2013) and
30 the Far East Organization.

32 **Competing interests**

33 The authors have no conflicts of interest to declare.

References

- 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.
- Białaszek, W., Marcowski, P., Ostaszewski, P., 2017. Physical and cognitive effort discounting across different reward magnitudes: Tests of discounting models. *PLoS ONE*, 12, e0182353–26.
- Boksem, M.a.S., Meijman, T.F., Lorist, M.M., 2006. Mental fatigue, motivation and action monitoring. *Biol Psychol*, 72, 123-132.
- Boksem, M.a.S., Tops, M., 2008. Mental fatigue: Costs and benefits. *Brain research reviews*, 59, 125-139.
- Bonnelle, V., Manohar, S., Behrens, T., Husain, M., 2016. Individual Differences in Premotor Brain Systems Underlie Behavioral Apathy. *Cerebral Cortex*, 26, 807–819.
- Buckner, R.L., Krienen, F.M., Castellanos, A., Diaz, J.C., Yeo, B.T.T., 2011. The organization of the human cerebellum estimated by intrinsic functional connectivity. *Journal of Neurophysiology*, 106, 2322–2345.
- 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. *Journal of Neuroscience*, 33, 1706-1713.
- 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. *Journal of Neuroscience*, 28, 5519-5528.
- 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, e1002598-28.
- Chong, T.T.-J., Bonnelle, V., Husain, M., 2016. Quantifying motivation with effort-based decision-making paradigms in health and disease. *Progress in Brain Research*, 229, 71-100.
- Coull, J.T., Frackowiak, R.S.J., Frith, C.D., 1998. Monitoring for target objects: activation of right frontal and parietal cortices with increasing time on task. *Neuropsychologia*, 36, 1325–1334.
- Craig, A.D.B., 2009. How do you feel — now? The anterior insula and human awareness. *Nature Reviews Neuroscience*, 10, 59–70.
- Esterman, M., Grosso, M., Liu, G., Mitko, A., Morris, R., Degutis, J., 2016. Anticipation of Monetary Reward Can Attenuate the Vigilance Decrement. *PLoS ONE*, 11, e0159741–19.
- Gergelyfi, M., Jacob, B., Olivier, E., Zenon, A., 2015. Dissociation between mental fatigue and motivational state during prolonged mental activity. *Frontiers in Behavioral Neuroscience*, 9.
- Goebel, R., Esposito, F., Formisano, E., 2006. Analysis of functional image analysis contest (FIAC) data with brainvoyager QX: From single-subject to cortically aligned group general linear model analysis and self-organizing group independent component analysis. *Human Brain Mapping*, 27, 392–401.
- Greve, D.N., Fischl, B., 2009. Accurate and robust brain image alignment using boundary-based registration. *NeuroImage*, 28, 63–72.
- Hockey, G.R., 2013. *The psychology of fatigue: work, effort and control*, Cambridge, Cambridge University Press.

- 1 Hopstaken, J.F., Van Der Linden, D., Bakker, A.B., Kompier, M.a.J., 2014. A multifaceted
2 investigation of the link between mental fatigue and task disengagement. 52, 305-315.
- 3 Kanfer, R., Ackerman, P.L., 1989. Motivation and cognitive abilities: An
4 integrative/aptitude-treatment interaction approach to skill acquisition. *Journal of*
5 *Applied Psychology*, 74, 657-690.
- 6 Klein-Flügge, M.C., Kennerley, S.W., Friston, K., Bestmann, S., 2016. Neural Signatures of
7 Value Comparison in Human Cingulate Cortex during Decisions Requiring an Effort-
8 Reward Trade-off. *The Journal of Neuroscience*, 36, 10002-10015.
- 9 Klein-Flügge, M.C., Kennerley, S.W., Saraiva, A.C., Penny, W.D., Bestmann, S., 2015.
10 Behavioral modeling of human choices reveals dissociable effects of physical effort
11 and temporal delay on reward devaluation. *Plos Computational Biology*, 11,
12 e1004116.
- 13 Kurniawan, I.T., Seymour, B., Talmi, D., Yoshida, W., Chater, N., Dolan, R.J., 2010.
14 Choosing to make an effort: the role of striatum in signaling physical effort of a
15 chosen action. *Journal of neurophysiology*, 104, 313-321.
- 16 Langner, R., Eickhoff, S.B., 2013. Sustaining attention to simple tasks: a meta-analytic
17 review of the neural mechanisms of vigilant attention. *Psychological Bulletin*, 139,
18 870–900.
- 19 Libedinsky, C., Massar, S.a.A., Ling, A., Chee, W.Y., Huettel, S.A., Chee, M.W.L., 2013.
20 Sleep Deprivation Alters Effort Discounting but not Delay Discounting of Monetary
21 Rewards. *Sleep*, 36, 899-904.
- 22 Lim, J., Choo, W.-C., Chee, M.W.L., 2007. Reproducibility of changes in behaviour and
23 fMRI activation associated with sleep deprivation in a working memory task. *Sleep*,
24 30, 61-70.
- 25 Lim, J., Dinges, D.F., 2008. Sleep Deprivation and Vigilant Attention. *Annals of the New*
26 *York Academy of Sciences*, 1129, 305-322.
- 27 Lim, J., Wu, W.-C., Wang, J., Detre, J.A., Dinges, D.F., Rao, H., 2010. Imaging brain fatigue
28 from sustained mental workload: An ASL perfusion study of the time-on-task effect.
29 *NeuroImage*, 49, 3426–3435.
- 30 Ma, N., Dinges, D.F., Basner, M., Rao, H., 2015. How Acute Total Sleep Loss Affects the
31 Attending Brain: A Meta-Analysis of Neuroimaging Studies. *Sleep*, 38, 233-240.
- 32 Massar, S.a.A., Csathó, Á., Van Der Linden, D., 2018. Quantifying the motivational effects
33 of cognitive fatigue through effort-based decision making. *Frontiers in Psychology*, 9,
34 843.
- 35 Massar, S.a.A., Libedinsky, C., Weiyan, C., Huettel, S.A., Chee, M.W.L., 2015. Separate and
36 overlapping brain areas encode subjective value during delay and effort discounting.
37 *NeuroImage*, 120, 104-113.
- 38 Massar, S.a.A., Lim, J., Huettel, S.A., 2019a. Sleep deprivation, effort allocation and
39 performance. *Progress in Brain Research*, 246, 1–26.
- 40 Massar, S.a.A., Lim, J., Sasmita, K., Chee, M.W.L., 2019b. Sleep deprivation increases the
41 costs of attentional effort: Performance, preference and pupil size. *Neuropsychologia*,
42 123, 169-177.
- 43 Massar, S.a.A., Lim, J., Sasmita, K.S., Chee, M., 2016. Rewards Boost Sustained Attention
44 through Higher Effort: A Value-based Decision Making Approach. *Biological*
45 *Psychology*, 120, 21-27.
- 46 Mcguire, J.T., Botvinick, M.M., 2010. Prefrontal cortex, cognitive control, and the
47 registration of decision costs. *Proceedings of the National Academy of Sciences of the*
48 *United States of America*, 107, 7922–7926.
- 49 Meyniel, F., Sergent, C., Rigoux, L., Daunizeau, J., Pessiglione, M., 2013.
50 Neurocomputational account of how the human brain decides when to have a break.

- 1 *Proceedings of the National Academy of Sciences of the United States of America*,
2 110, 2641–2646.
- 3 Müller, T., Apps, M.a.J., 2019. Motivational fatigue: A neurocognitive framework for the
4 impact of effortful exertion on subsequent motivation. *Neuropsychologia*, 123, 141–
5 151.
- 6 Myerson, J., Green, L., Warusawitharana, M., 2001. Area under the curve as a measure of
7 discounting. *Journal of the Experimental Analysis of Behavior*, 76, 235–243.
- 8 Otto, T., Zijlstra, F., Goebel, R., 2014. Neural correlates of mental effort evaluation—
9 involvement of structures related to self-awareness. *Social, Cognitive and Affective
10 Neuroscience*, 9, 307–315.
- 11 Parro, C., Dixon, M.L., Christoff, K., 2018. The neural basis of motivational influences on
12 cognitive control. *Human Brain Mapping*, 1–15.
- 13 Parvizi, J., Rangarajan, V., Shirer, W.R., Desai, N., Greicius, M.D., 2013. The will to
14 persevere induced by electrical stimulation of the human cingulate gyrus. *Neuron*, 80,
15 1359–1367.
- 16 Pessiglione, M., Vinckier, F., Bouret, S., Daunizeau, J., Le Bouc, R., 2017. Why not try
17 harder? Computational approach to motivation deficits in neuro-psychiatric diseases.
18 *Brain*, 141, 629–650.
- 19 Peters, J., Miedl, S.F., Büchel, C., 2012. Formal Comparison of Dual-Parameter Temporal
20 Discounting Models in Controls and Pathological Gamblers. *PLoS ONE*, 7, e47225.
- 21 Prevost, C., Pessiglione, M., Metereau, E., Clery-Melin, M.-L., Dreher, J.-C., 2010. Separate
22 Valuation Subsystems for Delay and Effort Decision Costs. *Journal of Neuroscience*,
23 30, 14080–14090.
- 24 Schwartz, G.E., 1978. Estimating the dimension of a model. *Annals of Statistics*, 6, 461–464.
- 25 Shenhav, A., Botvinick, M.M., Cohen, J.D., 2013. The expected value of control: an
26 integrative theory of anterior cingulate cortex function. *Neuron*, 79, 217–240.
- 27 Van Dongen, H.P.A., Belenky, G., Krueger, J.M., 2011. Investigating the temporal dynam-
28 ics and underlying mechanisms of cognitive fatigue. In: Ackerman, P.L. (ed.)
29 *Cognitive fatigue: multidisciplinary perspectives on current research and future
30 applications*. Washington, DC USA: American Psychological Association.
- 31 Vassena, E., Holroyd, C.B., Alexander, W.H., 2017. Computational Models of Anterior
32 Cingulate Cortex: At the Crossroads between Prediction and Effort. *Frontiers in
33 Neuroscience*, 11, 716.
- 34 Vyazovskiy, V.V., Olcese, U., Hanlon, E.C., Nir, Y., Cirelli, C., Tononi, G., 2011. Local
35 sleep in awake rats. *Nature*, 472, 443–447.
- 36 Wang, C., Ong, J.L., Patanaik, A., Zhou, J., Chee, M.W.L., 2016. Spontaneous eyelid
37 closures link vigilance fluctuation with fMRI dynamic connectivity states.
38 *Proceedings of the National Academy of Sciences of the United States of America*,
39 113, 9653–9658.
- 40 Warm, J.S., Parasuraman, R., 2007. Cerebral hemodynamics and vigilance. In: Parasuraman,
41 R. & Rizzo, M. (eds.) *Neuroergonomics the brain at work*. New York: Oxford
42 University Press. 46–158.
- 43 Warm, J.S., Parasuraman, R., Matthews, G., 2008. Vigilance requires hard mental work and
44 is stressful. *Human Factors*, 50.
- 45 Westbrook, A., Braver, T.S., 2015. Cognitive effort: A neuroeconomic approach. *Cognitive,
46 Affective, & Behavioral Neuroscience*.
- 47 Yeo, B.T.T., Krienen, F.M., Sepulcre, J., Sabuncu, M.R., Lashkari, D., Hollinshead, M.,
48 Roffman, J.L., Smoller, J.W., Zöllei, L., Polimeni, J.R., Fischl, B., Liu, H., Buckner,
49 R.L., 2011. The organization of the human cerebral cortex estimated by intrinsic
50 functional connectivity. *Journal of Neurophysiology*, 106, 1125–1165.

- 1 Yeo, B.T.T., Tandi, J., Chee, M.W.L., 2015. Functional connectivity during rested
2 wakefulness predicts vulnerability to sleep deprivation. *NeuroImage*, 111, 147-158.
3 Zenon, A., Sidibe, M., Olivier, E., 2015. Disrupting the Supplementary Motor Area Makes
4 Physical Effort Appear Less Effortful. *The Journal of Neuroscience*, 35, 8737–8744.
5