



Sleep deprivation increases the costs of attentional effort: Performance, preference and pupil size



Stijn A.A. Massar, Julian Lim, Karen Sasmita, Michael W.L. Chee*

Centre for Cognitive Neuroscience, Neuroscience and Behavioral Disorders Program, Duke-NUS Medical School, Singapore

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ABSTRACT

Sleep deprivation (SD) consistently degrades performance in tasks requiring sustained attention, resulting in slower and more variable response times that worsen with time-on-task. Loss of motivation to exert effort may exacerbate performance degradation during SD. To test this, we evaluated sustained performance on a vigilance task, combining this with an effort-based decision-making task and pupillometry. Vigilance was tested at rest and after sleep deprivation, under different incentive conditions (1, 5 or 15 cents for fast responses). Subsequently, preference measures were collected from an effort-discounting task, in which a commensurate reward was offered for maintaining attentional performance for different durations (1, 5, 10, 20 or 30 min). Vigilance was impaired during SD, in a manner modulated by reward value. Preference metrics showed that the value of available rewards was discounted by task duration, an effect compounded by SD. Pupillometry revealed that arousal was modulated during SD in a value-based manner, and moment-to-moment fluctuations in pupil diameter were directly predictive of performance. Together, these data demonstrate that attentional performance can be interpreted within a value-based effort allocation framework, such that the perceived cost of attentional effort increases after sleep deprivation.

1. Introduction

Sleep deprivation (SD) adversely affects many cognitive functions including memory, attention and decision making (Killgore, 2015; Krause et al., 2017; Lim and Dinges, 2010). Sustained attention - the ability to detect and respond to infrequently occurring target stimuli over long durations (Mackworth, 1968) - is by far the most consistently and severely affected cognitive domain (Goel et al., 2013; Lim and Dinges, 2010; Lowe et al., 2017). As such, tests of sustained attention have become integral in assessing behavior following sleep deprivation.

Even in a well-rested state, engaging sustained attention is subjectively effortful, and performance demonstrates time-on-task degradation (Warm et al., 2008) that is exacerbated by SD (Lim and Dinges, 2008). Responses become slower, more variable, and are punctuated by microsleeps (Basner and Dinges, 2011).

Neuroimaging studies show that prefrontal and parietal cortical brain areas and subcortical areas (including thalamus, striatum and midbrain) involved in supporting sustained attention (Langner and Eickhoff, 2013) show diminished activation during SD that declines over continued task performance (Asplund and Chee, 2013; Zhu et al., 2017). In the traditional resource depletion account of vigilance performance, degraded vigilance and reduced brain activation are marks of

reduced processing capacity in SD. The latter would arise from continuous engagement of task related neural circuits resulting in depletion of the required resources to perform optimally (Warm et al., 2008).

The effects of such resource depletion might be exacerbated if available resources are not optimally employed. While reward motivation can improve sustained attention performance (Esterman et al., 2014; Massar et al., 2016), fatigue from sleep loss and time-on-task may affect the motivation to perform. Consequently, sleep deprived subjects may choose to invest less effort into task performance and to withdraw processing resources (Lim and Dinges, 2008; Mackworth, 1968). Interestingly, this idea fits well with recent theories in the field of effort-based decision making whereby performance is influenced by a continuous cost-benefit analysis (Kurzban et al., 2013). According to this framework, performance is dependent on a value-based decision to invest effort into the task according to the value of associated rewards (Kool and Botvinick, 2014; Westbrook and Braver, 2015). Although this effort-allocation hypothesis has been proposed in several models of fatigue and SD, systematic empirical investigation is lacking.

In the current study, we tested the value-based effort-allocation hypothesis through three inter-related approaches. First, we examined whether sustained attention performance is influenced by rewards provided for successful task completion. For this purpose, participants

* Corresponding author.

E-mail address: michael.chee@duke-nus.edu.sg (M.W.L. Chee).

performed a psychomotor vigilance task (PVT; Dinges and Powell, 1985) under three levels of reward. Importantly, we set out to test whether performance decline due to SD and time-on-task would be modulated in a value-based fashion. Secondly, we recorded pupil diameter as a physiological marker of attentional effort and arousal. Lastly, we used a formal effort-based decision-making task to test how SD state and task duration were weighed into the decisions to engage in task performance.

2. Methods

2.1. Participants

Twenty-six subjects were recruited from the university population (mean age [stdev] = 22.8 y [3.5]; 16 females). All participants reported to be healthy, non-smoker, have no history of neurological or psychiatric disorder (including sleep disorders), and to not use any long-term medication. Participants had regular habitual sleep schedules (i.e. 6:30–9 h/night) and did not qualify as extreme morning or evening-type (Horne and Östberg, 1976). Objective sleep history was monitored for 5 days prior to the experimental sessions using wrist actigraphy (Actiwatch2; Philips Respironics; Andover, MA, USA).

2.2. Sleep deprivation procedures

Participants took part in two experimental sessions spaced about one week apart in counterbalanced order. During the rested wakefulness (RW) session, participants came into the lab in the evening and were given 9 h of sleep opportunity (10 p.m.–7 a.m.). Experimental test started at 8 a.m. the next morning. In the sleep deprivation (SD) session participants arrived at the same time but were kept awake during the night. Throughout the SD night participants performed hourly vigilance test (grad-CPT; Esterman et al., 2013) and sleepiness ratings (Karolinska Sleepiness Scale; Gillberg et al., 1994). Test in the SD session commenced at 6 a.m.

2.3. Motivated vigilance task

In both sessions, participants performed a sustained attention task (Psychomotor Vigilance Task: PVT; Dinges and Powell, 1985) under different reward conditions (See Fig. 1A). The test started with a baseline run, in which no rewards were provided. Participants were seated in front of a computer screen, with their head positioned on a chinrest. They were instructed to fixate on a central dot, and to respond as quickly as possible to the appearance of a running millisecond counter (ISI: 2–10 s; uniformly distributed). After the baseline run, participants performed three runs in which they earned rewards for fast responses. In the low reward run they could earn 1 cent, in the medium

reward run they earned 5 cents, and in the high reward run they could earn 15 cents per fast responses. All runs lasted for 10 min, resulting in approximately 80 trials per run (mean [stdev] = 79.6 [4.4]). The response criterion for the rewarded runs was set to the median RT in an individual's baseline run. A prior study using this procedure demonstrated that performance improved in a value-dependent manner (Massar et al., 2016). The order of the rewarded runs was counterbalanced between subjects, but for each subject, this order was kept fixed between the RW and SD sessions. Pupil size was continuously monitored during performance of the attention task via an eyetracker (Tobii X60; Tobii AB, Danderyn, Sweden).

2.4. Discounting task

To explicitly test whether participants incorporated the costs and benefits of sustaining attention in their decisions, a discounting task was performed, where monetary rewards were offered for performing the PVT for a given duration (See Fig. 1B). Following the vigilance task runs, participants were presented with a series of choices. On each trial, they indicated their preference between performance of a short duration PVT for a small amount of money (Shorter Smaller or SS option), or a longer duration PVT for a larger amount of money (\$12; Longer Larger or LL option). The reward amount for the SS option was varied from trial to trial using an adjusting staircase for five consecutive iterations (Libedinsky et al., 2013; Massar et al., 2015; Massar et al., 2016). Indifference points were calculated as the average of the lowest accepted SS amount and the highest rejected SS amount, for LL durations of 1, 5, 10, 20, and 30 min (presented in intermixed fashion). These points represent the SS value that individuals considered as equally valuable as a \$12 reward at the cost of performing the task at a given LL task duration. This procedure was repeated twice resulting in a total of 50 trials. Subjective values were calculated as the average of the indifference points for each LL duration. The area under the resulting discounting curve was quantified as a model-free summary metric of the level of discounting (larger area under the curve denotes less steep discounting; Myerson et al., 2001). Choices were incentive-compatible and one randomly drawn choice was executed following the discounting task (PVT was performed for the chosen duration, in return for the indicated reward).

Discounting tasks are widely used in behavioral decision making as a method to quantify the subjective costs of different decision variables (e.g. risk, delay, effort; Green and Myerson, 2004; Kowal et al., 2007). To ensure that participants in our study did not base their choices on the costs of delayed rewards, they were instructed that after the choice task, they had to stay in the lab for 30 min. Their choices would determine how much time, out of the 30 min, they would spend on performing the sustained attention task. However, irrespective of the PVT duration, they would receive their reward only after 30 min.

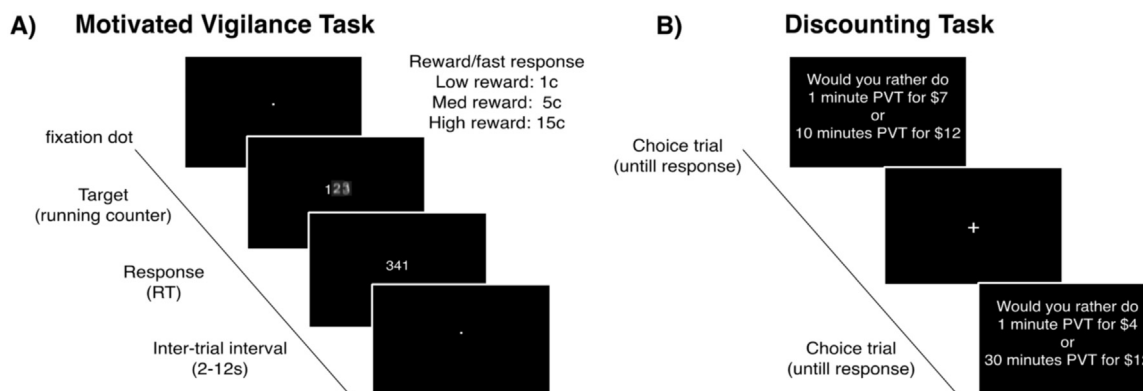


Fig. 1. Task procedures for the (A) Motivated Vigilance Task, participants performed 10 min runs of the Psychomotor Vigilance Task under low, medium and high reward conditions, and (B) Discounting Task, participants made sequential choices between task duration/reward options.

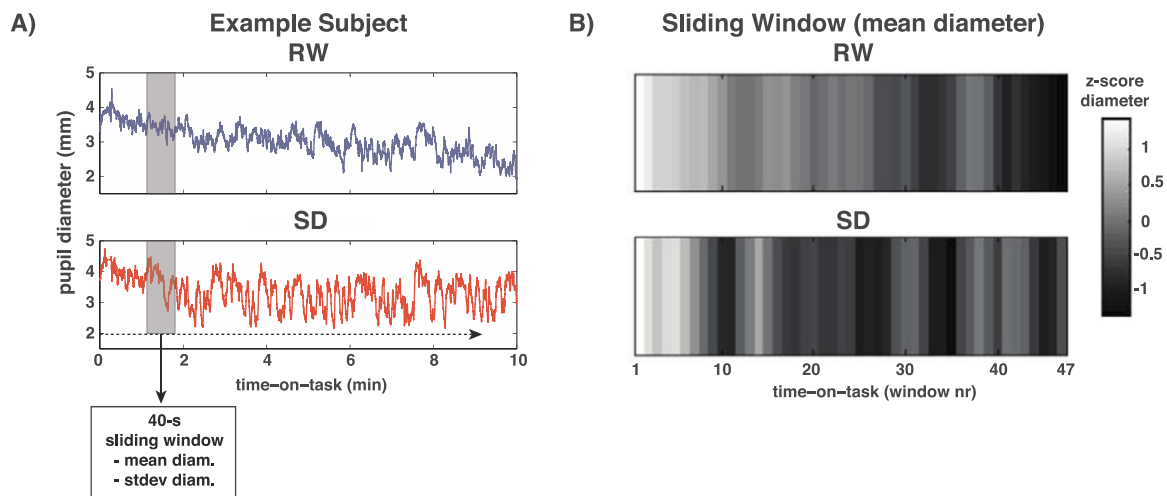


Fig. 2. Single-subject pupillometry analysis. (A) Raw pupillometry time series for example subject in RW (blue) and SD (red) in LOW reward condition. (B) Sliding window time series for mean diameter.

Participants' understanding of this procedure was checked after verbal instructions using visual analogue scales (See [Supplementary Materials](#)). There was no indication that they had incorrect understanding of the instruction during either the RW or SD session. Data for one subject was not correctly saved due to script error. Statistical analysis is based on the remaining subjects ($N = 25$).

2.5. Pupillometry

Pupil diameter is influenced by the ascending arousal system and is a sensitive indicator of sleepiness (Wilhelm et al., 1998). Pupil diameter is also known to scale with cognitive effort (Kahneman, 1973), being larger when participants are performing more difficult tasks (Kahneman and Beatty, 1966), or if they are more engaged in performance (Hopstaken et al., 2014). Pupil size was recorded during performance of the Motivated Vigilance Task runs at a sampling frequency of 60 Hz. Pupil diameter and variability were quantified as the mean and standard deviation in 40-sec moving windows (Fig. 2). Portions of missing data due to blinks or eye-closures were linearly interpolated, and resulting time series were low-pass filtered with a 10 Hz cut-off. Recording failed for two subjects due to inability of the eye-tracker algorithm to detect the pupil. Three more subjects had excessive artifacts (> 60%) in at least one of the task runs. These subjects were excluded from analysis. The final sample size for pupil analysis was $N = 21$.

2.5.1. GLM analysis

To analyze the effects of sleep state, time-on-task and reward on pupil diameter, average diameter and log-transformed standard deviation of pupil diameter were quantified in 40 s sliding windows (step-size = 12 s; See Fig. 2) (van den Brink et al., 2016) for each PVT run for each subject. Data in each window were z-scored across all task runs for each participant separately. Two separate GLM analyses were conducted with diameter and variability as independent variables respectively (See Fig. 5). Five separate regressors were included. One regressor coded for the main effect of sleep state (RW = 0, SD = 1). Two regressors coded the effect of time-on-task for the RW runs and for the SD runs separately. Two additional regressors were included, coding for the reward level per run in RW and in SD separately. At a second level, individual parameter estimates (Beta-values) were contrasted against zero (one sample *t*-tests), to determine whether each separate regressor had a significant effect on pupil diameter. Furthermore, the effect of sleep state on the parameter estimates for time-on-task and reward was tested by directly contrasting their respective RW and SD estimates (paired *t*-tests). This approach allowed us to extract parameter

estimates for the effects of time-on-task and of reward in RW and SD separately, and thereby to directly contrast their contributions between sleep states. Furthermore, it allowed us to apply identical analytical approaches to pupil diameter and to pupil variability as dependent variables.

2.5.2. Trial-by-trial analysis

To examine the moment-to-moment contribution of pupil diameter to vigilance performance, the analysis was focused on the 1-second window directly preceding the target stimuli. Trials were manually checked for artifacts and only trials with minimal missing data within the 1-sec pre-stimulus window were included in further analysis. This left a minimum of 31 trials per run for all participants. Pupil diameter and response speed for the remaining trials were z-scored across all task runs for each participant separately, and linear trial-by-trial correlations were calculated for each run and each subject separately. Resulting correlation coefficients were Fisher-z transformed and compared to zero (one-sampled *t*-tests) to examine whether there was any systematic group-level correlation (positive or negative) between pre-stimulus pupil diameter and response speed. Furthermore, to probe the respective effects of sleep and motivation on these (Fisher-z transformed) correlations, data were subjected to a Sleep state (RW, SD) \times Reward (1, 5, 15c) repeated measures ANOVA.

3. Results

3.1. SD-related performance decline is modulated by reward value

To determine how SD and reward affect performance in the Motivated Vigilance Task we examined two metrics highly sensitive to SD (Basner and Dinges, 2011), i.e. attentional lapses (responses with RT > 500 ms) (Fig. 3, upper panels) and response speed (1/RT) (Fig. 3, lower panels).

As expected, poorer performance during SD was characterized by more lapses ($F_{1,25} = 33.02$, $p < .001$) and slower response speed ($F_{1,25} = 76.40$, $p < .001$) compared to RW. In addition, overall performance was modulated by reward (lapses: $F_{2,50} = 8.97$, $p < .001$; response speed: $F_{2,50} = 18.25$, $p < .001$), where better performance accompanied higher reward (Fig. 3, left panels).

Of interest, there was an interaction between state and reward (lapses: $F_{2,50} = 6.17$, $p = .004$; response speed: $F_{2,50} = 2.99$, $p = .059$). To interpret the found interactions, we quantified the size of the SD-effect as the SD-RW difference score at each reward level (Fig. 3, middle panels). Paired *t*-tests showed that the SD-effect was more

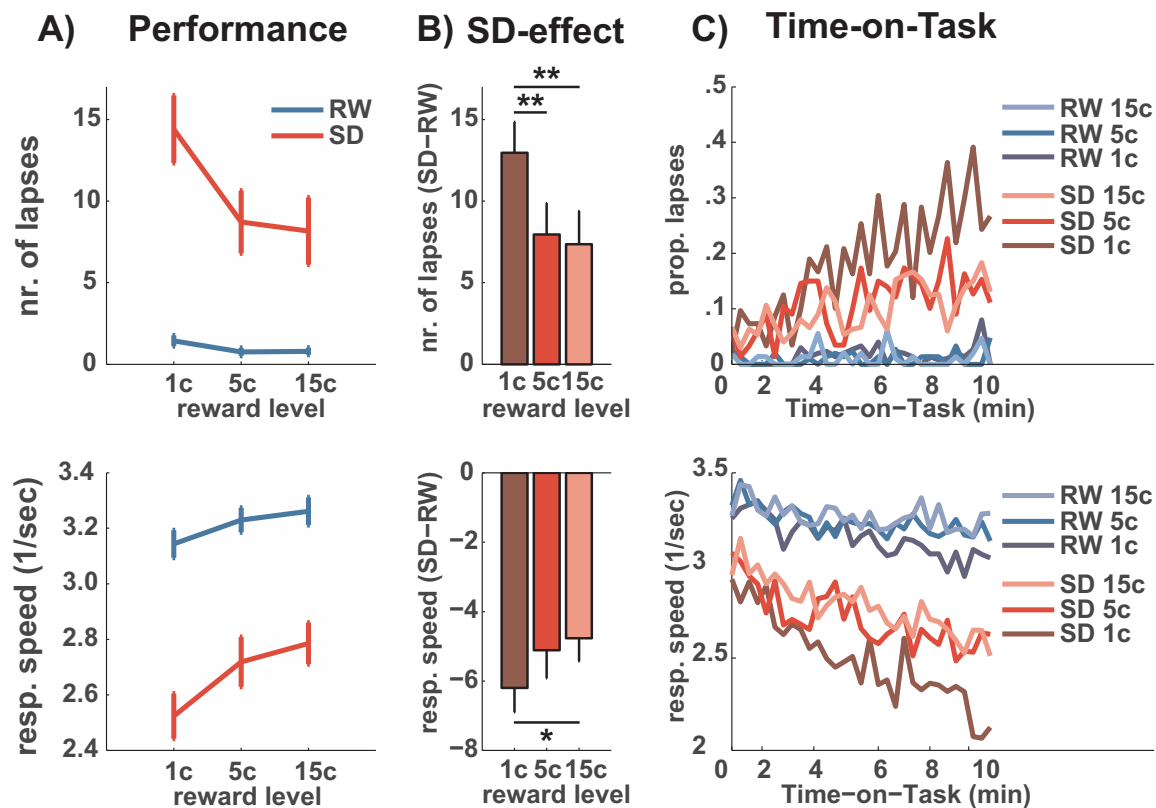


Fig. 3. Performance in the Motivated Vigilance Task for attentional lapses (upper panels) and response speed (lower panels), with (A) mean performance per reward level and per sleep state, (B) SD-RW difference scores, and (C) Time-on-Task effects. * $p < .05$, ** $p < .01$.

pronounced in the low reward runs compared to the higher reward runs (lapses [low > med]: $t_{25} = 2.89$ $p = .008$; lapses [low > high]: $t_{25} = 2.90$ $p = .008$; response speed [low < high]: $t_{25} = 2.45$, $p = .02$). These results suggest that, in the sleep deprived state, reward motivation can partially alleviate SD related performance decline.

Importantly, there was no evidence that faster performance in the higher reward runs resulted from a lower response threshold. False start responses (i.e. button presses in the absence of a target) did not increase in number as a function of reward ($F_{2,50} = 2.19$, $p = .12$). If anything, they showed a numerical decrease with higher rewards (See Suppl. Fig. 1), showing that reward led to improved performance without causing a speed-accuracy trade off (Manohar et al., 2015). Furthermore, performance of the current sample was compared to that of an unrewarded control sample ($N = 76$; previously reported in Yeo et al., 2015). This analysis showed that while performance in the low reward run was comparable to that of typical (un-incentivized) performance, faster response speed and fewer lapses were found in the medium and high reward runs (See Suppl. Fig. 2).

3.2. Performance decline due to time-on-task is modulated by sleep state and reward value

A characteristic of sustained attention tasks is that performance declines with time-on-task. One explanation for this observation is the depletion of cognitive resources, that is typically exacerbated by SD (Lim and Dinges, 2008). To examine whether reward motivation could influence time-on-task decline in the RW and SD states, we extracted linear trend coefficients for response speed over time-on-task in each task run (Fig. 3, right panels). Performance declined with time-on-task in all conditions, and this decline was steeper during SD compared to RW ($F_{1,25} = 10.29$, $p = .004$). Time-on-task related performance decrement was significantly attenuated by higher reward in both states ($F_{2,50} = 4.89$, $p = .01$), indicating that value-based allocation of

resources provides a compelling alternative to a pure resource depletion account of performance dynamics under sleep deprivation or increasing time-on-task.

3.3. Subjective value of attentional performance is reduced during SD

3.3.1. Model-free analysis

In the discounting task, individuals' subjective value of the offered reward amount was determined from the point at which they were indifferent between the SS amount and the LL amount, at different durations of the proposed PVT. These indifference points were plotted on a discounting curve (Fig. 4A), and showed an overall decrease of subjective value with longer proposed task duration. The area under the discounting curve (a summary metric of the extent of discounting) was significantly reduced during SD compared to RW ($t_{24} = 2.12$, $p = .04$; Fig. 4 B&C). Participants thus considered the larger reward subjectively less valuable if they had to perform the sustained attention task for a longer duration, particularly during SD.

3.3.2. Model-based analysis

An issue of contemporary interest is whether the discount function associated with effort-based decision making follows the same shape as that found in delay discounting (Bialaszek et al., 2017; Chong et al., 2017; Klein-Flügge et al., 2016, 2015). In order to explore this, we fitted different discounting models to the individual choice data (See Supplementary Materials for details). The choice data were best explained by a sigmoid model (Fig. 4D-E; as proposed for effort-discounting by Klein-Flügge et al., 2015). Resulting model parameters were square root transformed to correct for non-normality (Peters et al., 2012) and compared between sleep states. The p-parameter (inflection point) was shifted leftwards after sleep deprivation (i.e. participants started discounting at shorter proposed durations of task performance; $t_{24} = 2.13$, $p = .04$; see Fig. 4F). This corroborated the findings of

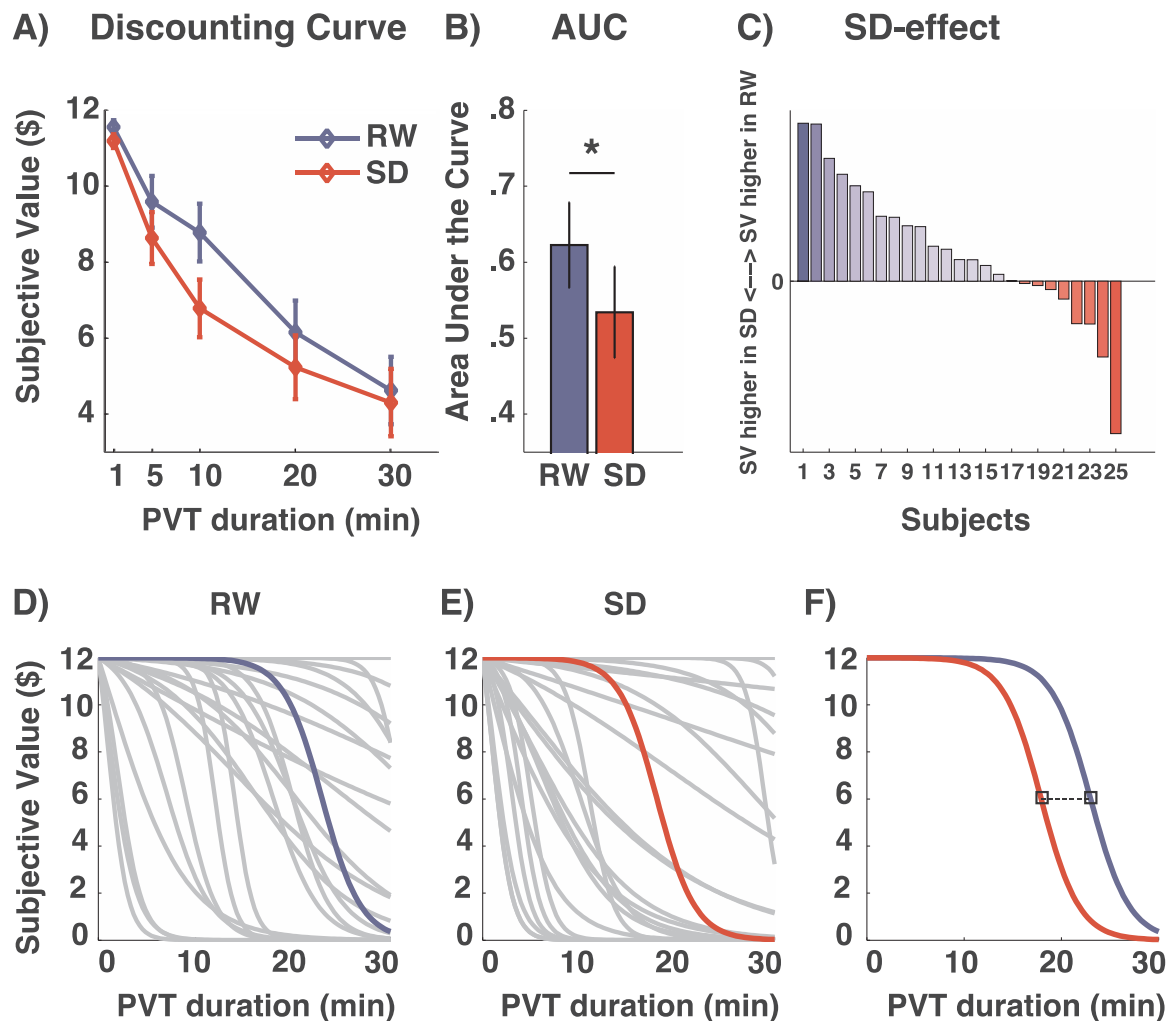


Fig. 4. Behavioral preference in the Discounting Task, with (upper panels) model-free analysis, and (lower panels) model-based analysis. (A) discounting curves in RW and SD, (B) Group average area under the Discounting Curves for RW and SD (\pm SEM; AUC = area under the curve), and (C) distribution of individual RW-SD difference (SV = Subjective Value). D & E) Individual (grey lines) and average model fits in RW (blue line) and SD (red line). F) Average model fits (dotted line indicates shifted inflection point from RW to SD).

model-free analysis, showing that participants show a systematic shift in their willingness to perform the PVT for longer durations during SD. Additionally, the beta-parameter was found to be significantly lower in SD compared to RW ($t_{24} = 2.10$, $p = .047$), indicating that choices were less strictly based on the subjective value function (more random) in SD. No difference in the slope of the sigmoid function (k-parameter) were found between sleep states ($t_{24} = .10$, $p = .92$).

3.4. Pupil diameter reveals value-based effort allocation during attentional performance

The influence of sleep state, reward and time-on-task were analyzed using a general linear model (GLM; Fig. 5). Results showed that overall pupil diameter did not significantly differ between RW and SD runs ($t_{20} = -1.5$, $p = .15$). However, as with the behavioral findings, pupil diameter decreased with time-on-task, both in RW ($t_{20} = -5.86$, $p < .001$) and in SD ($t_{20} = -2.95$, $p = .008$). Central to the current investigation, pupil diameter was significantly modulated by reward in SD ($t_{20} = 4.42$, $p < .001$), but not in RW ($t_{20} = 1.38$, $p = .18$). A direct contrast (equivalent to a Reward \times Sleep state interaction) confirmed that reward modulation was stronger in the SD runs compared to the RW runs ($t_{20} = 2.14$, $p = .045$). In contrast, pupil variability was affected by SD and time-on-task, but was not meaningfully modulated by reward motivation (See Suppl. Fig. 3). These findings

suggest that participants could regulate their arousal levels in a value-based manner, particularly during a low arousal state such as SD. Such arousal regulation likely reflects the allocation of attentional effort to uphold performance.

3.5. Pre-stimulus pupil diameter predicts trial-by-trial response speed

To test whether fluctuations in pupil diameter were related to performance, trial-by-trial baseline diameter was extracted from a 1-second window directly prior to target presentation (Fig. 6A). For each task run, the trial-by-trial correlation between pre-stimulus diameter and response speed was calculated (Fig. 6B), and at a group level, the z-transformed r-values were compared to zero (Fig. 6C). There was a positive correlation between pre-stimulus pupil diameter and response speed. Trials with larger baseline pupil sizes were associated with faster responses. Interestingly, these associations were stronger in SD compared to RW ($F_{1,20} = 17.82$, $p < .001$), and with a marginally significant reduction with higher reward levels ($F_{2,50} = 3.0$, $p = .064$).

4. Discussion

In this study, we examined how the value-based allocation of attentional effort influences sustained attention performance after sleep deprivation. Results from the motivated vigilance task showed that

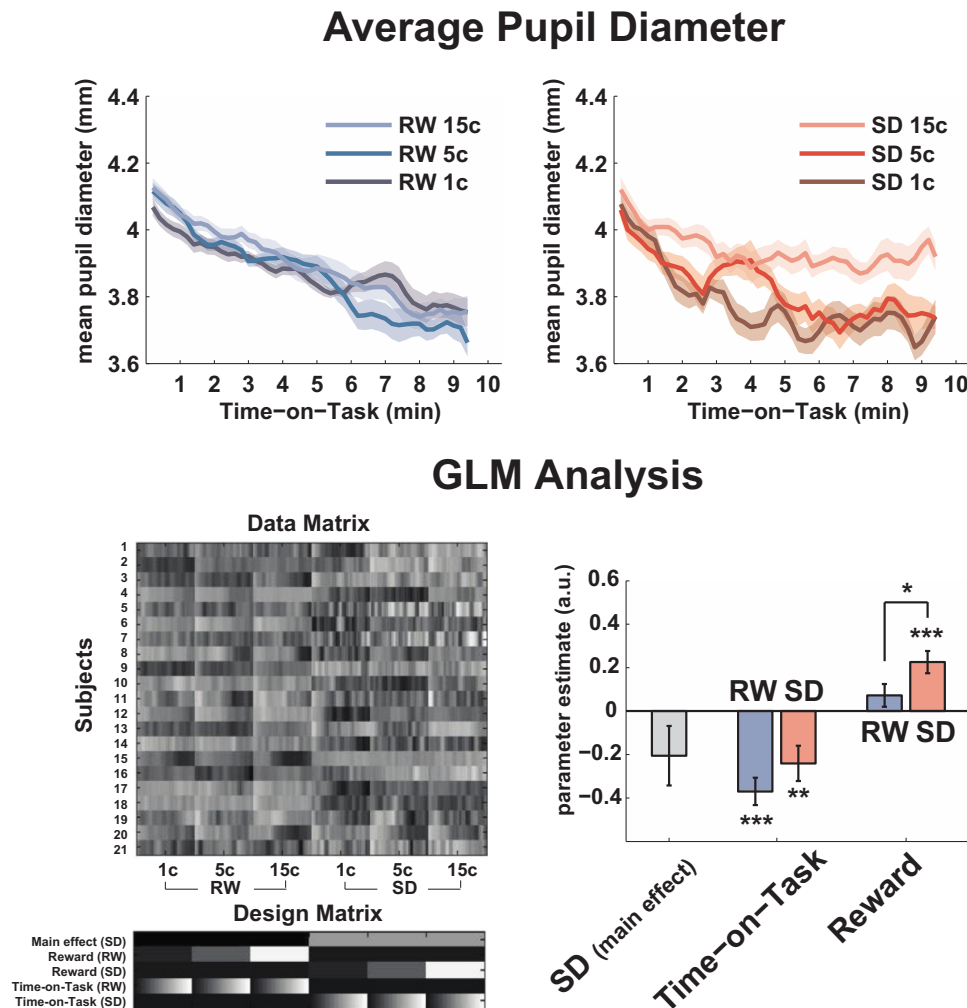


Fig. 5. Average pupil diameter over the runs of the Motivated Vigilance Task (upper panels; shaded areas denote within-subjects SEM). GLM data and design matrix (lower left), and group average regression coefficients (\pm SEM) for the SD main effect, Time-on-Task, and Reward regressors (lower right). * $p < .05$, ** $p < .01$, *** $p < .001$.

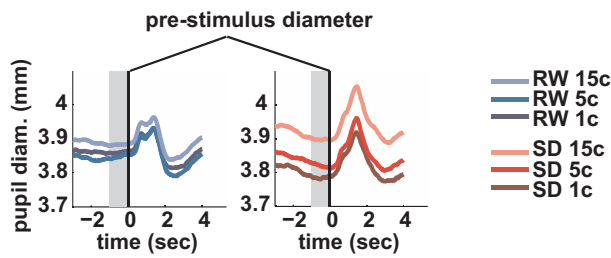
performance was modulated based on the incentive value. Both overall performance and maintenance over time improved with higher rewards. Strikingly, this reward-modulation effect was more pronounced after SD compared to RW. This indicates that impaired vigilance after SD is the combined result of reduced attentional capacity, and diminished motivation, rather than only a capacity reduction (or depletion of resources). This behavioral pattern was closely paralleled by pupillometric data, showing a value-based reward modulation that was mainly apparent during the SD session. Previous research has shown that SD can result in increased reward-related brain activation (Gujar et al., 2011; Mullin et al., 2013; Venkatraman et al., 2007, 2011). Finally, a formal test of effort-based decision making indicated that participants devalued a given reward, in accordance to the required task duration particularly during SD. These findings support the hypothesis that, performance in tasks high in attention demands involve balancing cost of effort required to maintain alertness, and the benefit of attaining a rewarded outcome (Kurzban et al., 2013). Our findings indicate that this effort/value weighing function is shifted during SD, such that attentional effort is allocated preferentially to tasks that are deemed sufficiently valuable. We posit that this effect of SD on effort allocation reflects a motivational deficit that may exacerbate the well-known detrimental effects of SD on ‘processing capacity’.

4.1. A neuro-economic framework of motivational decline under SD

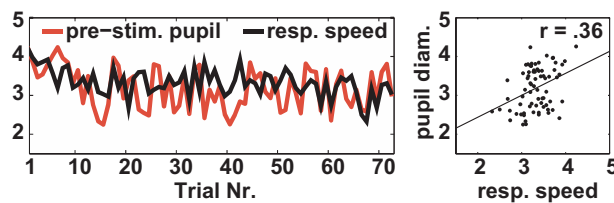
Although reduced motivation is a commonly observed consequence of SD, there has been little systematic research into its effects. One reason for this is that motivation is a subjective construct that is hard to quantify other than by self-report. In recent years, a growing body of literature has adopted the view that motivation reflects the willingness to exert effort to reach performance goals (Chong et al., 2016). Specific tasks have been developed to quantify this (i.e. effort-based decision-making tasks). By making incentive-compatible choices about effortful courses of behavior, individuals weigh the costs of effort against the value of the potential gains (Kool and Botvinick, 2014; Westbrook and Braver, 2015), and compute a subjective value of the effortful choice. A decision to engage in effortful action tends to follow only if the reward is deemed sufficiently valuable. A specific neural circuitry is involved in making such computations (including ACC and anterior insula; Prevost et al., 2010). Using such an effort-based decision-making task, our findings suggest that SD devalues the benefit of exerting effort.

Effort-based decisions are heavily influenced by motivational factors, and affected in conditions characterized by a loss of motivation (e.g. Major Depression Disorder, anhedonia, apathy; Cley-Melin et al., 2011; Hershenberg et al., 2016; Treadway et al., 2012). Furthermore, they are susceptible to the limits of cognitive capacity. Westbrook et al. (2013) found that elderly discounted effortful rewards more strongly

A) Average target-locked pupil trace



B) Trial-by-trial correlation (example run)



C) Average correlation

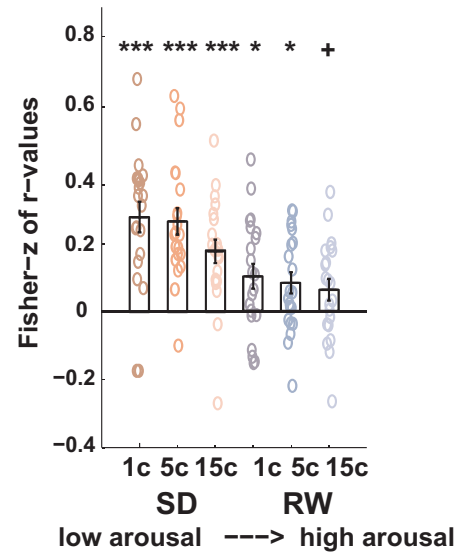


Fig. 6. Correlation between pre-stimulus pupil diameter and performance. (A) Stimulus locked-pupil traces, with pre-stimulus baseline diameter (grey areas). (B) Trial-by-trial correlation between pre-stimulus pupil diameter and response speed for an example run. (C) Fisher-z transformed correlation coefficients for individual runs (colored dots), and group average (bars; \pm SEM). + $p = .055$, * $p = .01$, *** $p < .001$.

than young adults. In the context of sleep deprivation, a few experimental studies have looked at changes in effort allocation. Engle-Friedman et al. (2003) found that sleep-deprived subjects tended to prefer performing less effortful mathematics problems compared to a group of well-rested subjects. In an earlier study from our lab, we found that sleep deprived subjects discounted the value of monetary rewards more strongly than well rested ones if the rewards were contingent on performance on an effortful typing task. In contrast sleep deprivation did not alter behavior in a delay-discounting task (Libedinsky et al., 2013).

Our current data concur and suggest that, under SD, the subjective value of effortful attentional performance is diminished, leading subjects to withdraw processing resources from performance if rewards are not sufficiently high. It is interesting to note that several theoretical models of performance decline with fatigue (not specific to SD) have proposed a very similar role for priority-based resource allocation processes in performance maintenance (Boksem and Tops, 2008; Hockey, 1997; Kanfer and Ackerman, 1989).

4.2. Task duration as an effort-related cost

When evaluating the cost of effort in decision making, it is important to separate the influence of effort from other potential costs (e.g. temporal delay or risk; Apps et al., 2015; Kool and Botvinick, 2014). In the effort-based decision task used here, effort was defined as the proposed duration of PVT performance following the choice task. While it is clear that sustaining attention for longer time is experienced as more effortful (Warm et al., 1996), some points must be noted. First of all, in this portion of the experiment, participants were rewarded based on the accepted duration of performance, not based on performance level (e.g. response speed/accuracy). This procedure has the advantage that it removes the risk of not getting the full reward (i.e. probability discounting) from participant's choice behavior. However, the exact level of performance (i.e. effort invested in task performance) is not controlled for. By using task duration as a measure of effort,

temporal discounting may be introduced into choice behavior. Previous reports indicate no change in temporal discounting after SD (Acheson et al., 2007; Libedinsky et al., 2013; Massar and Chee, 2015), but we took pains to minimize the influence of time by equating the experiment duration (i.e. fixing the delay to reward to 30 min). Interestingly, the resulting discounting curve followed a shape that has previously been associated with effort discounting (sigmoid) rather than temporal or probability discounting (Klein-Flügge et al., 2015).

4.3. Reward-based pupil modulation reflects volitional regulation of arousal

Pupillometric variables are known to be sensitive to manipulations of sleep state and arousal, showing smaller diameter and higher variability after SD (Wilhelm et al., 1998; Yoss et al., 1970). Pupil diameter reflects the dynamic interplay between the effects of sympathetic and parasympathetic inputs (Lowenstein and Loewenfeld, 1964), fluctuating with activity in the norepinephrinergic (NE) Locus Coeruleus (LC) in animals (Joshi et al., 2016; Reimer et al., 2016), and in human resting state fMRI (Murphy et al., 2014). The correlation between pupil fluctuations and LC activity is potentially established through a common arousal regulation pathway, originating from the ventrolateral medulla (Nieuwenhuis et al., 2011). Pupil diameter corresponds with the (attentional) effort that a subject is exerting (Kahneman, 1973). Larger pupil size is reflective of higher task difficulty (Kahneman and Beatty, 1966), task engagement and reward motivation (Hopstaken et al., 2014). Notably, evidence from animal electrophysiology shows that such effort-related increase in pupil diameter is associated with increased LC activation (Varazzani et al., 2015).

In the present study we found that, during SD, pupil diameter was modulated in a value-based manner. This suggests that participants were able to volitionally regulate their arousal levels to meet the task goals. The observed modulation presumably reflects the top-down regulation of brainstem arousal areas (including the LC), by higher cortical areas (Coull, 1998). Regions such as the ACC and anterior

insula, which are also involved in effort valuation, are thought to implement such top-down control, as they are consistently activated during the execution and anticipation of effortful tasks (Croxson et al., 2009; Engstrom et al., 2015). Interestingly, a recent study found that dynamic pupil dilations after sleep restriction correlate with activation in the brain's salience network (including ACC and anterior insula; Schneider et al., 2016). The authors proposed that top-down regulation of arousal, in order to maintain wakefulness, could be a possible mechanism underlying this correlation. Our current data support this interpretation, showing that SD-related decline in arousal can be countered if one is sufficiently motivated.

4.4. Trial-by-trial pupil fluctuations are predictive of performance

Besides the modulation of tonic pupil diameter, the sleep deprived state was further characterized by a high variability in pupil diameter over time. These fluctuations in arousal became more pronounced with time-on-task and importantly, were directly related to fluctuations in performance. This closely aligns with the idea that increased behavioral variability after SD reflects unstable maintenance of the wake state due to mounting homeostatic sleep pressure and the intrusion of sleep-initiating mechanisms (wake state-instability; Doran et al., 2001). It is important to note that overall, pupil variability was not significantly modulated by reward. Alternating periods of low and high arousal occurred across all levels of reward. It is therefore plausible that motivated effort can partially counter declining arousal while one is awake, but cannot fully prevent the occurrence of micro-sleeps (Horne and Pettitt, 1985).

Other studies reporting the relationship between pupil size and performance have yielded mixed findings. To date, studies have reported positive (van den Brink et al., 2016), negative (Gilzenrat et al., 2010; Unsworth and Robison, 2016), and U-shaped correlations (Murphy et al., 2011; van den Brink et al., 2016). Most studies however, have been performed in the well-rested state, describing only a narrow range of arousal. In the current study, correlations were stronger in SD compared to RW. It is therefore possible that the relatively smaller variability in RW performance and pupil diameter impairs estimation of the pupil-performance association. Alternatively, it is possible that association between arousal and performance is non-linear. Theories about LC-NE activity have proposed that performance follows an inverted U-shape, with poor performance at low arousal levels, optimal performance at intermediate arousal levels and declining performance at very high arousal levels (Aston-Jones and Cohen, 2005). It is likely that the SD manipulation in the current study drives the subjects towards the lower end of the arousal spectrum. Within this range (before the peak of the inverted U), positive correlations would be more expected. In line with this interpretation, correlations were found to be stronger (more positive) in the SD state compared to RW.

5. Conclusions

The primary aim of this study was to systematically examine how motivational shifts due to SD affect sustained attention performance. Using traditional response time metrics, and novel discounting methods, we found that the willingness to exert attentional effort is reduced during SD. This was evident from the reduced subjective value of performance-related rewards, and a more preferential allocation of resources to high-value tasks runs. SD-related performance deficits could be partially mitigated if higher rewards were available. Pupillometric data showed that reward motivation was associated with a regulation of arousal that was directly linked to performance improvement. In all, the current findings provide clear evidence that part of the detrimental effects of SD on sustained attention performance are attributable to reduced motivation. Such a measured approach to effort allocation may be particularly important when processing resources are scarcer due to SD.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.neuropsychologia.2018.03.032>.

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