Preserved calibration of persistence based on delay-timing distribution during sleep deprivation

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SUMMARY

We frequently encounter decisions where we have to determine whether to wait for a certain reward delayed for an uncertain duration or to move on. The appropriate decision depends upon the underlying temporal distribution of the delay. With some distributions it is best to be completely persistent, whereas in others it is more appropriate to abandon waiting after a certain period of time. The current study examined whether the ability to form temporal expectations and adjust persistence accordingly is compromised by sleep deprivation. Participants performed a willingness-to-wait task either in a well-rested state or after a night of total sleep deprivation. Participants had to decide either to wait for a larger reward or to abandon waiting in favour of a smaller immediate reward. Delays were drawn from either a uniform distribution, where being persistent yields maximal returns, or from a heavy-tailed distribution, where occasional long delays render full persistence suboptimal. In spite of increased sleepiness and decreased vigilance, sleep-deprived participants were able to adjust waiting time appropriate to the experienced timing distribution. Additionally, sleep deprivation did not affect the foreperiod effect, indicating intact perception of conditional probability of temporal events and ability to adjust preparation accordingly.

INTRODUCTION

One of the most trying decisions we make each day is to determine whether or not to wait for something worthwhile when it is unclear how long we need to wait. For example: do we wait for a delayed train or do we walk out of the station to look for a cab? In some situations, how long we should wait before moving on is known (e.g. if the duration of the train delay is announced), but at other times we simply do not know (e.g. if announcements are not made or are unreliable). Under the latter circumstance, one can turn to temporal expectations derived and updated from experience. Recent studies have shown that persistence when waiting for an event to occur is strongly dependent upon expectations of the delay duration (McGuire and Kable, 2013) Decision-makers adjust their persistence dynamically based on the experienced statistical distribution of delays (McGuire and Kable, 2012). Relevant to the present work, insufficient sleep can affect decision-making negatively by impairing our ability to integrate prior outcome information accurately into later decisions (Olson *et al.*, 2014; Whitney *et al.*, 2015). However, whether or not the ability to calibrate persistence based

on experienced delays is affected by sleep deprivation has not been studied previously.

Prior studies examining how total sleep deprivation (TSD) affects intertemporal choice have yielded mixed results. In an intertemporal choice task, subjects are asked repeatedly to choose between a smaller but immediately available reward and a delayed but larger reward that is received days to months later. Two prior studies found no evidence for altered choice behaviour during TSD (Acheson *et al.*, 2007; Libedinsky *et al.*, 2013). However, increased impulsive choice was found in a task in which participants had to wait out delays (in the seconds range) in accordance with choices made in each trial (Reynolds and Schiffbauer, 2004). It is possible that choice preference under TSD is particularly sensitive to experienced delays, possibly arising from alterations in time perception (Casini *et al.*, 2013; Reynolds and Schiffbauer, 2004). Critically, in all three prior studies, delay durations were declared explicitly. It is presently unclear if TSD would compromise one's ability to form accurate delay expectations from experienced timing distributions.

In the current study we employed a task that tested persistence under different experienced timing distributions

(McGuire and Kable, 2012). Participants were given the opportunity to harvest monetary rewards within a fixed amount of time (10 min). Rewards were preceded by a delay of unknown duration. On each trial, participants could wait for the delay to pass and receive the reward. Alternatively, they had the option to stop waiting at any time and to receive an immediate small reward. Optimal performance in this task is critically dependent upon the distribution of delay durations. In one condition, the likelihood of reward delivery would increase upon longer waiting times, making it desirable to wait for each trial to complete. In the other condition, longer waiting times were associated with decreasing probability of the reward being available soon, promoting abandoning the wait after some delay. Performance on this task thus depends essentially on the capability to form appropriate temporal expectations from the experienced distributions of the delays. Participants in our study performed this task under both sleep-deprived and well-rested states.

METHODS

Participants

Twenty-nine participants were recruited [13 females; mean age, standard deviation (SD) = 22.28 (2.05)] through the university's online bulletin board. Participants had no history of neurological or psychiatric disorders, and were not taking any long-term medication. They did not have a history of any sleep disorder and had good sleeping habits (reporting an average sleep duration of at least 6.5 h per night during the past month). Medication, alcohol or caffeine was disallowed 24 h prior to the test sessions. Volunteers were paid for their contribution.

Procedure

All participants underwent one rested wakefulness session (RW) and one total sleep deprivation session (TSD) that were spaced at least 1 week apart in a counterbalanced order. One week prior to the first experimental session, participants underwent briefing/training. They practised short versions of the cognitive tasks, and received an actiwatch for sleep monitoring (Actiwatch 2; Philips Respironics, Andover, MA, USA). Sleeping habits were monitored to ensure that all participants maintained a regular schedule of 6.5–9 h of sleep daily for at least 5 days prior to the experimental sessions. During the RW session participants arrived at the laboratory at 08:00 hours after having had a normal night of sleep. Subsequently, the experimental procedure started with the performance of one run of the psychomotor vigilance task (PVT; Dinges and Powell, 1985), followed by two runs of the willingness-to-wait task (in both uniform and heavy-tailed distribution). Subjective sleepiness was measured by the Karolinska Sleepiness Scale (KSS; Akerstedt and Gillberg, 1990) and the Stanford Sleepiness Scale (SSS; Hoddes *et al.*, 1973) prior to the start of the experiment. For the TSD

session subjects came into the laboratory at 21:00 hours on the evening before the experiment. Participants were kept awake overnight by a research assistant. Hourly assessments of subjective sleepiness and vigilance performance were conducted until 06:00 hours the next morning, after which the experimental tasks were conducted. This procedure was approved by the institutional review board of the National University Singapore, and all participants provided written informed consent prior to participation.

Psychomotor vigilance task

Vigilance was tested using the psychomotor vigilance task (PVT; Dinges and Powell, 1985). Participants were seated in front of a computer screen and were instructed to respond as quickly as possible to the appearance of a running millisecond counter. These stimuli were separated by intertrial intervals (ITIs) that were drawn from a uniform random distribution (2–10 s). We measured attentional lapses [reaction-times (RTs) > 500 ms], which have been found to be a highly reliable measure of decreased vigilance during sleep deprivation (Basner and Dinges, 2011).

Willingness-to-wait task

The willingness-to-wait task was based on the task described by McGuire and Kable (2012). Participants were shown a coloured circle that was illuminated for a random period. After the delay period had passed the circle would turn grey and participants could collect a reward (¢15) by pressing a response button. Alternatively, at any moment before the end of the delay, they could instantly stop waiting by pressing a different button and receive a smaller immediate reward (¢1). Each trial was followed by a 2-s ITI, and participants had 10 min to gather as much money as possible. Participants performed two runs of this task, each under a different delay distribution. In the uniform distribution (UD) delay, durations ranging from 0 to 16 s were equally probable (see Fig. 1). In this condition delays never lasted beyond 16 s, therefore the expected remaining delay decreased with time elapsed. Consequently, optimal returns could be obtained by waiting for the reward on all trials (see Data S1). In the heavy-tailed distribution (HTD), delays were drawn from a distribution in which the majority of trials had a short delay time, but on the remaining trials a disproportionally long delay was presented (truncated generalized Pareto distribution; $\kappa = 8$, $\sigma = 3.4$, and $\theta = 0$, truncated at 90 s; see Fig. 1). With this distribution, the expected remaining waiting time would increase as a function of time already spent waiting. Therefore, optimal returns would be obtained by terminating the wait beyond a certain delay. In contrast, being persistent beyond that time would result in lower total rewards because time spent waiting on a long-delay reward could be spend more fruitfully, harvesting more short-delay rewards (see Data S1 for waiting time and expected return functions). The probability distribution functions and cumulative distribution functions of the
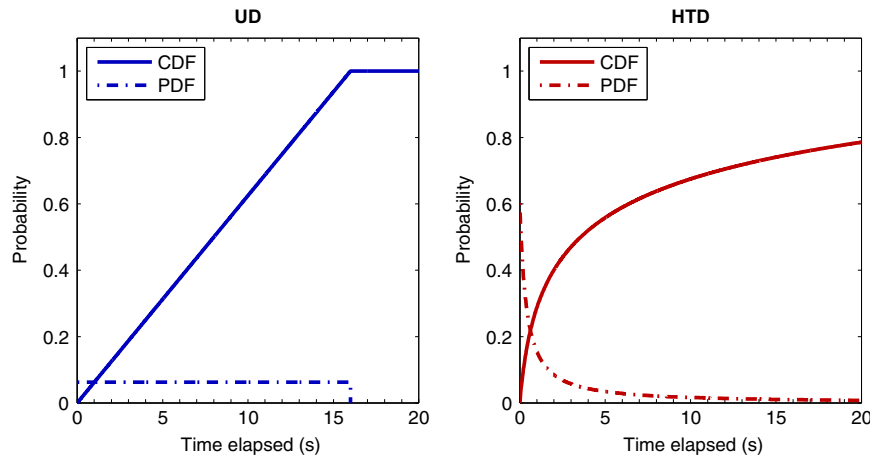
Figure 1. Probability density functions (PDF) and cumulative distribution functions (CDF) for the uniform (UD) and heavy-tailed distributions (HTD) during the first 20 s.

uniform and heavy-tailed distribution conditions are illustrated in Fig. 1. The order of conditions was counterbalanced between subjects, but kept constant over the within-subject RW and TSD sessions. Different-coloured circle stimuli were used for the uniform distribution run and for the heavy-tailed distribution run. Participants practised an abbreviated version of the task (5 min per distribution) during the training session. They were instructed that the temporal distribution of both tasks differed and were encouraged to explore the timing properties in each run independently (see Data S1 for full instructions).

Analysis

Persistence analysis

Trials in which the participant chose to stop waiting before the reward was delivered were classified as 'quit-trials'. Trials in which the participant waited throughout the full delay to receive the reward were classified as 'persistent trials'. Trials with excessively long RTs (>2 s) were classified as 'lapses'. Using this criterion, 1.3% (UD) and 0.13% (HTD) of trials were identified as lapses during the RW session, and 11.9% (UD) and 5.9% (HTD) of trials in TSD. Lapses are important to identify, as it cannot be determined unambiguously whether participants were waiting deliberately through the full delay in these trials or if they were temporarily disengaged from the task as a result of microsleep. Lapse trials were not included in further analysis.

Based on the stop times in quit-trials and the total delay durations in persistent trials, Kaplan–Meier survival curves were constructed separately for each run and each participant (Kaplan and Meier, 1958). Persistent trials were considered right-censored because they only provide information about the participant's willingness to wait until the time of reward delivery. In quit-trials, the time of termination was considered to reflect directly the participant's willingness to wait, and these trials were coded as 'deaths'. For statistical comparison of the two distributions, survival analyses were restricted to a 0–15-s interval for which there were observations in both conditions. The area under the survival curves (AUC) served as a summary measure of willingness to wait, with a large AUC indicating a more persistent choice pattern and a small AUC indicating a more impatient choice pattern. AUCs were entered into a distribution (uniform, heavy-tailed) × state (RW, TSD) repeated-measures analysis of variance (ANOVA).

Timing-based RT analysis

Performance in the willingness-to-wait task depends upon the ability to form temporal expectations from the presented distributions. The formation of such temporal expectations has also been studied from a perspective of temporal preparation (Nobre *et al.*, 2007). Research on implicit time perception has demonstrated that reaction-times can be modulated strongly by the interval between a preceding warning signal and an imperative signal (the foreperiod). In situations in which foreperiod durations are distributed randomly and uniformly, faster responses typically follow longer foreperiods (Nickerson, 1965; Niemi and Näätänen, 1981). The foreperiod effect is thought to reflect a higher state of preparedness at time-points with the highest probability of a critical event (conditional upon the fact that it has not yet occurred; Niemi and Näätänen, 1981; Nobre *et al.*, 2007). Notably, the foreperiod effect is attenuated strongly (or absent) when the foreperiod distribution has a long right tail (e.g. exponential distribution; Baumeister and Joubert, 1969; Cui *et al.*, 2009; Kong *et al.*, in press; Näätänen, 1970; Zahn and Rosenthal, 1966). The foreperiod effect can be observed in simple reaction-time tasks such as the PVT, and is found to be robust against (or even enhanced by) the effects of sleep deprivation (Kong *et al.*, in press; Tucker *et al.*, 2009; Wilkinson, 1990).

Here we examined the foreperiod effect both in the PVT and in the willingness-to-wait task. In the PVT we quantified

the foreperiod effect following previous work (Kong *et al.*, in press). RTs were binned according to their preceding ITI (short <4.67 s; medium >4.67 s <7.33 s; long >7.33 s). Median RTs for each bin were extracted for each subject, and response speed was compared across bins and sleep states. In the willingness-to-wait task, defining the width of the foreperiod bins was less straightforward. In order to create bins that contained sufficient trials under both distributions, a bin cut-off was set at 2 s (i.e. short foreperiod: delay ≤2 s; long foreperiod: delay >2 s). Note that the exact number of trials per bin depended upon the properties of the distributions and on individual persistence levels (i.e. an impatient choice pattern resulted in fewer trials in the long foreperiod bin). A minimum threshold of five trials per bin for each distribution and each session was set. Participants who did not have sufficient trials for each bin, distribution and session were excluded from this RT analysis. Median reaction-times per bin were determined and entered into a bin (short foreperiod, long foreperiod) × distribution (uniform, heavy-tailed) × state (RW, TSD) repeated-measures ANOVA.

RESULTS

Sleepiness and psychomotor vigilance

Sleep deprivation resulted in a significant increase in subjective sleepiness, slower reaction-times and increased number of lapses in the PVT relative to rested wakefulness (Table 1), indicating that the sleep deprivation manipulation was successful. The increase in false alarms during TSD did not reach significance (Table 1).

Willingness-to-wait task

Lapses

Similar to the PVT, the number of lapses in the willingness-to-wait task increased in the TSD session (see Table 1). There

Table 1 Mean (standard deviation) scores for subjective sleepiness scales and psychomotor vigilance performance

	RW	TSD	t-value	P-value
Sleepiness				
KSS	2.69 (1.23)	6.79 (1.88)	12.02	<0.001
SSS	1.93 (0.75)	4.93 (1.31)	11.85	<0.001
PVT				
Median RT	323.7 (31.4)	389.4 (71.0)	6.26	<0.001
False alarms	1.86 (2.0)	5.45 (13.10)	1.44	0.16
Lapses	3.79 (3.37)	15.14 (13.13)	5.31	<0.001
Willingness-to-wait task				
Lapses UD	0.55 (0.63)	4.52 (5.32)	3.95	<0.001
Lapses HTD	0.07 (0.26)	3.14 (3.91)	4.16	<0.001

KSS, Karolinska Sleepiness Scale; SSS, Stanford Sleepiness Scale; RT, reaction time; RW, rested wakefulness; TSD, total sleep deprivation; UD, uniform distribution; HTD, heavy-tailed distribution.
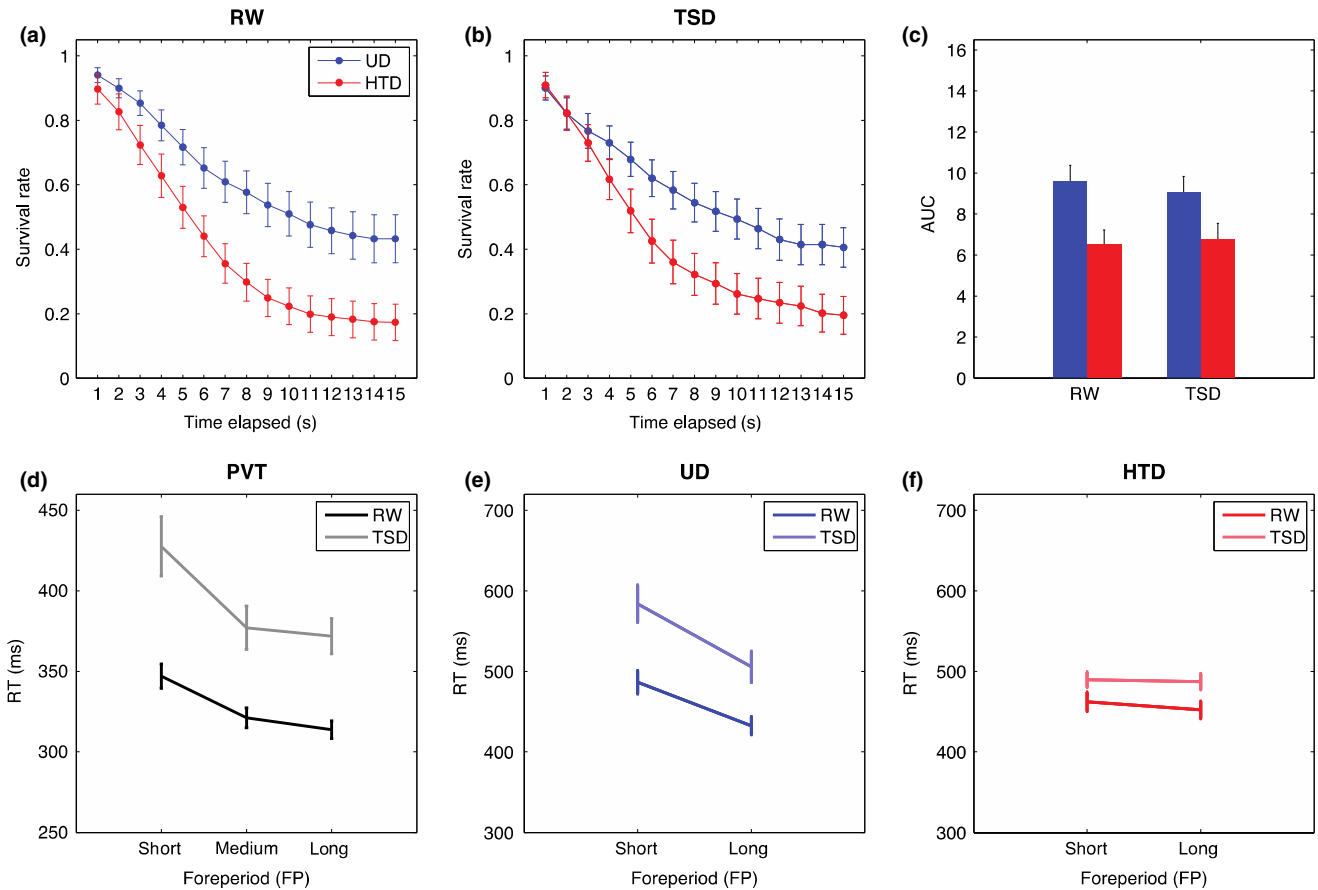
was a significant main effect of state on lapses ($F_{(1,28)} = 22.92$, $P < 0.001$) and a borderline effect of distribution ($F_{(1,28)} = 3.89$, $P = 0.058$), with more lapses in the uniform compared to heavy-tailed distribution conditions. No significant interaction between state and distribution was found [$F_{(1,28)} = 0.85$, not significant (NS)].

Persistence analysis

Participants were more persistent in the uniform distribution compared to the heavy-tailed distribution condition in both sessions, evidenced by differences in AUC of survival curves ($F_{(1,28)} = 12.01$, $P < 0.001$) that were similar across RW and TSD sessions ($F_{(1,28)} = 0.74$, NS; Fig. 2a–c).

Foreperiod analysis

Psychomotor vigilance task

There was a significant main effect of state on reaction-times ($F_{(1,28)} = 39.43$, $P < 0.0001$), and additionally a clear foreperiod effect across both states ($F_{(2,56)} = 24.24$, $P < 0.0001$). The foreperiod effect was larger during TSD compared to RW, as evident from a significant state × bin interaction ($F_{(2,54)} = 4.14$, $P < 0.05$; see Fig. 2). These findings concur with recent observations from an independent study in our laboratory (Kong *et al.*, in press).

Willingness-to-wait task

Analysis of the foreperiod effect in the willingness-to-wait task was based on RTs collected during persistent trials. In order to create temporal bins that contained sufficient trials for each foreperiod and temporal distribution, two bins were defined (short foreperiod <2 s and long foreperiod >2 s). Seven participants had fewer than five trials in one of the bins and were excluded from analysis, resulting in data from 22 subjects being analysed (see Fig. 2e,f). Critically, there was a significant foreperiod by temporal distribution interaction ($F_{(1,21)} = 11.22$, $P < 0.005$). Separate ANOVAs were performed for the uniform and heavy-tailed distribution conditions. Faster RTs were found in the long foreperiod bin in the uniform distribution condition ($F_{(1,21)} = 11.11$, $P < 0.005$), but not in the heavy-tailed distribution condition ($F < 1$, NS). Sleep deprivation did not affect the foreperiod effect, as was evident from the absence of significant state × temporal bin interactions ($Fs < 1$, NS). A potential limitation of using the same bin cut-off across distributions is that it resulted in disproportionately few long foreperiod trials in the heavy-tailed distribution. As such, we performed an additional analysis in which bin cut-offs were defined separately for both distributions, such that there were approximately equal numbers of short and long foreperiod trials. The foreperiod effects remained significant in the uniform distribution, and remained absent in the heavy-tailed distribution condition (see Data S1).

Figure 2. Survival curves for the uniform (UD) and heavy-tailed (HTD) distributions in (a) rested wakefulness and (b) sleep deprivation, and (c) corresponding area under the curves. Reaction-times per foreperiod bin in (d) the psychomotor vigilance task and the willingness-to-wait task under (e) uniform distribution and (f) heavy-tailed distribution. Error bars represent ±1 standard error of the mean.

DISCUSSION

The current study shows that the ability to form temporal expectations is conserved after a night of total sleep deprivation, as was the ability to adjust persistence while waiting for a reward. Participants remained highly persistent in the decision task when reward signals were distributed uniformly, but abandoned waiting after a short duration when they encountered the heavy-tailed distribution. The ability to perceive timing distribution was also evident from the intact foreperiod effect in both the PVT and the willingness-to-wait task with uniform distribution. Such behaviour was maintained, despite clear evidence of sleepiness, slower response times and increased behavioural lapses.

Calibration of persistence based on timing distribution is preserved during sleep deprivation

Analysis of the survival curves demonstrated that participants chose consistently to wait longer for rewards when delays were distributed uniformly, whereas waiting was terminated earlier when delays were distributed in a heavy-tailed fashion. This pattern of choice is similar to that found by other studies (McGuire and Kable, 2013), and demonstrates

that participants indeed calibrate their persistence according to the timing context. Importantly, this pattern was preserved under sleep deprivation. These findings have two implications. First, it appears that sleep deprivation does not change preferences for rewards that are discounted by a delay. Two previous studies found no changes in choice persistence under sleep deprivation using classical delay-discounting tasks (Acheson *et al.*, 2007; Libedinsky *et al.*, 2013). One study, however, reported increased impulsive choice in an experiential delay-discounting task (Reynolds and Schiffbauer, 2004).

We argued initially that the effects of sleep deprivation on intertemporal choice may be most prominent with experienced delays, as opposed to those encountered at a later time. The latter type of delay is encountered in intertemporal choice tasks where decisions involve either immediate rewards or ones to be received days to months later. Several studies have demonstrated that individual differences in choice impulsivity are related to differences in time perception (Baumann and Odum, 2012; Marshall *et al.*, 2014; Wittmann and Paulus, 2008). Moreover, changes in explicit time perception have been reported after sleep deprivation (Casini *et al.*, 2013; Kuriyama *et al.*, 2005; Poeppel and Giedke, 1970; Reynolds and Schiffbauer, 2004; Soshi *et al.*,

2010). Contrary to our initial expectation, we found that experienced delays do not necessarily lead to lower persistence during sleep deprivation.

Perception of implicit timing distribution is preserved during sleep deprivation

A second implication of the present findings is that the ability of human observers to assess implicit temporal distributions is not affected by sleep deprivation. In addition to the finding that distribution-sensitivity in choice persistence was preserved during sleep deprivation, further evidence for intact implicit time perception was found in reaction-time patterns. In both the PVT and in the willingness-to-wait task under the uniform distribution, reaction-times were faster when preceded by longer foreperiods. In contrast, reaction-times did not vary according to foreperiod under the heavy-tailed distribution in the willingness-to-wait task, where the conditional target probability does not rise monotonically with time elapsed (Cravo et al., 2011; Nickerson and Burnham, 1969). The foreperiod effect reflects increased attentional preparedness at time-points at which an imperative event is most likely to occur (Nickerson, 1965; Niemi and Näätänen, 1981), and has been attributed to strategic monitoring (Näätänen, 1970) or implicit learning mechanisms (Los et al., 2001).

The present findings indicate that temporal expectancy is preserved despite the deleterious effects of sleep deprivation and mental fatigue on vigilance (Kong et al., in press; Langner et al., 2010; Tucker et al., 2009). It is likely that the combination of intact tracking of conditional probability, intact sense of the passage of time and allocation of limited attention to later time-points of imperative events results in the preserved foreperiod effects during TSD. None of these processes need to be conscious or deliberately strategic, but they require intact integration of information across multiple trials, and may represent a passive combination when cognitive resources are impoverished in the sleep-deprived state. Hence, despite the intuitive notion that we 'tune out' during lapses, sleep-deprived participants retain the ability to keep track of the temporal features of a task.

CONCLUSION

The present study shows that the formation of temporal expectation based on implicit timing distributions is preserved during sleep deprivation. Despite clear increases in subjective sleepiness and impaired vigilant responding, both reward decision processes and temporal preparation remained sensitive to temporal distribution information in sleep-deprived individuals.

ACKNOWLEDGEMENTS

CONFLICT OF INTEREST

No conflicts of interest declared.

AUTHOR CONTRIBUTIONS

MWLC and SAAM conceived the design, SAAM performed the experiment; MWLC and SAAM wrote the paper.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Data S1. Supplementary Methods and Results.