A split-sleep schedule rescues short-term topographical memory after multiple nights of sleep restriction

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Abstract

Study Objectives: Chronic sleep restriction in adolescents is widespread, yet we know little about how to apportion the limited amount of sleep obtained to minimize cognitive impairment: should sleep occur only nocturnally, or be split across separate nocturnal and daytime nap periods? This is particularly relevant to hippocampal-dependent cognitive functions that underpin several aspects of learning.

Method: We assessed hippocampal function in four groups by evaluating short-term topographical memory with the four mountains test (4MT). All participants began with 9-hours nocturnal time-in-bed (TIB) for 2-days before following different sleep schedules over the next 3-days. Each day, one group had 5-hours nocturnal TIB (n=30), another, 6.5-hours nocturnal TIB (n=29), and a third had 6.5-hours split into 5-hours nocturnal TIB and a 1.5-hour TIB daytime nap (5.0+1.5h; n=29). A control group (n=30) maintained 9-hours nocturnal TIB. The 4MT was administered mid-afternoon (1.5-hours after awakening for those who napped).

Results: Performance of the 5.0h and 6.5h nocturnal TIB groups was significantly impaired relative to the 9.0h control group. Performance of participants on the split- sleep schedule (5.0+1.5h) did not significantly differ from controls.

Conclusions: These findings suggest that hippocampal function is sensitive to moderate multi-night sleep restriction, but deficits can be ameliorated by splitting sleep, at least for a period after waking from a daytime nap. While this split sleep schedule should not be considered a replacement for adequate nocturnal sleep, it appears to benefit the cognitive and neurophysiological functions that underpin learning in those who are chronically sleep deprived.

Keywords: sleep restriction, sleep deprivation, memory, spatial memory, topographical memory, split sleep, nap

Statement of significance

While many studies indicate that napping is beneficial to cognition, it remains unclear whether the nap itself leads to cognitive improvement, or if the same benefits are achievable by simply getting more nocturnal sleep instead. Here we show that splitting sleep between a nocturnal period and a daytime nap improves hippocampal-dependent cognitive function under conditions of chronic sleep restriction, even when total time available for sleep is controlled. In the absence of adequate nocturnal sleep, a split sleep schedule may optimize cognition.

Introduction

Chronic sleep restriction is associated with a wide range of physical and psychological deficits[1,2] and has become increasingly prevalent in adolescents.[3,4] In one study, less than

8% of high school students in the US reported obtaining optimal sleep[5], while populations in East Asia consistently obtain below 6h on weekday nights[6–8], well below the 8-10h recommended by the National Sleep Foundation[9]. While the consequences of sleep deficits on development and academic achievement can be substantial, questions remain as to the amount of sleep restriction that leads to cognitive impairment, which cognitive faculties and underlying neurophysiology are worst affected, and the extent to which interventions such as daytime naps can alleviate these deficits.

Most experimental research into the consequences of sleep loss on cognition have examined performance after a night of total sleep deprivation, which negatively impacts a wide range of cognitive functions[10]. Cognition that relies on prefrontal cortical function, such as working memory (WM) and executive function, is particularly sensitive to total sleep deprivation[11–13]. However, a night of total sleep loss rarely occurs outside of a laboratory setting. A more common pattern of partially restricted sleep across several consecutive days reduces alertness and sustained attention[7,8,14], but more complex cognitive operations such as working memory are less consistently affected[15]. Four nights of 5h time-in-bed (TIB) was found to impair WM and executive function (n-back task) in adolescents[7], but several other studies show resilience to similar schedules of chronic sleep restriction, for n-back[16] and verbal working memory[17] in adolescents, and visual working memory in adults[18,19].

It is widely recognized that extending nocturnal sleep in adolescents toward the recommended 8-10h[9] is critical to their long-term well-being, which may be achieved via methods such as delaying school start times[20]. Habitual napping may be another low cost and scalable way to relieve cognitive impairment arising from chronic sleep restriction[21]. Although the potentially helpful practice of splitting sleep across a nocturnal period and a short afternoon nap is common in some countries[22,23], only a handful of experimental studies

have examined the cognitive benefits of this practice. Psychomotor vigilance and processing speed were shown to decline with total sleep obtained within a 24-hour period, but splitting sleep into either nocturnal and afternoon nap periods[24], or two equivalent periods across 24h[25,26] in adults did not affect performance. These findings suggest that cognitive performance is determined by total time available for sleep, regardless of how that sleep is distributed.

Such findings seem at odds with observations that daytime naps enhance a number of cognitive operations, including attention[27–29], working memory[8] and long-term memory[30–33]. These benefits are thought to result from active processes taking place primarily during non-rapid-eye-movement (NREM) sleep that refresh the capacity to process information[34] and reorganize memory networks[31]. Critically, napping in these studies constitutes an additional period of sleep to supplement a fixed amount of nocturnal sleep, rather than splitting the total sleep obtained across 24-hours into nocturnal and nap periods. It therefore remains an open question as to whether a split sleep schedule is beneficial to cognition, particularly in cognitive domains such as working memory and long-term memory that are critical for effective learning. The present study aimed to explore this issue by assessing whether splitting sleep can alleviate cognitive impairments in chronically sleep deprived adolescents, with a focus on hippocampal-dependent memory functions.

The Four Mountains Test (4MT) is a delayed match-to-sample task that assesses short-term topographical memory, and is critically dependent on the hippocampus for processing viewpoint invariant (allocentric) spatial information[35–39]. In healthy adults, hippocampal volume correlates with 4MT ability[40], while performance is impaired in patients with conditions linked to hippocampal atrophy[35–39]. Notably, 4MT performance in patients with

fronto-temporal dementia is comparable to age matched controls[39]. This suggests the task is less reliant on WM functions typically ascribed to prefrontal cortex[11,12,41].

The 4MT has not previously been used in adolescents or in the context of sleep research. Performance on this task is directly relevant to behaviors that rely on a "cognitive map", such as spatial navigation, and it may provide a novel behavioral indication of hippocampal function under different schedules of chronic sleep restriction. Since the encoding of hippocampal-dependent episodic memories is sensitive to sleep deprivation[6,42,43] and benefits from daytime naps[32,33], we reasoned that the 4MT may show a similar impairment after chronic sleep restriction and benefit from a split sleep schedule.

To explore these questions, we compared 4MT performance with a non-hippocampal dependent test of working memory and executive function, the n-back task[44], in four groups of adolescents who underwent different schedules of chronic sleep restriction on 3 consecutive days. Groups with only 5-hours nocturnal TIB, 6.5-hours nocturnal TIB, or 5-hours nocturnal TIB with a 1.5-hour daytime nap opportunity were compared to a control group who had 9-hours nocturnal TIB (Fig. 1). Consistent with our prior work, n-back performance was not expected to differ between groups after only 3-nights of restricted sleep. We predicted a decline in 4MT performance with sleep loss, while the split sleep schedule was expected to enhance performance relative to the other two chronically sleep deprived groups.

Methods

Participants

120 adolescents between 15-19 years of age were selected from volunteers reporting no history of chronic or medical conditions, psychiatric illness or sleep disorders, were not habitual short sleep sleepers (> 6h actigraphically assessed average TIB), had a body mass index (BMI) ≤ 30, consumed <5 caffeinated beverages a day and had not travelled across >2 time zones one month prior to the study. Participants and parents provided written informed consent, in compliance with a protocol approved by the National University of Singapore Institutional Review Board, and received monetary compensation after completion.

Participants were randomised into two pairs of groups as part of the Need for Sleep 3 (NFS3: 9.0h and 5.0h groups)[6] and Need for Sleep 4 studies (NFS4: 6.5h and 5.0+1.5h groups). Two participants withdrew due to personal reasons or illness, leaving a final sample comprised of 118 participants (58 females, 16.3 ± 0.8 years [mean ± SD]). Groups did not differ in gender, BMI, consumption of caffeinated beverages, or on tests of non-verbal intelligence, morning-eveningness preference, levels of daytime sleepiness, symptoms of chronic sleep reduction, subjective sleep quality, self-reported and actigraphically assessed sleep habits, or levels of anxiety and depression ($p > 0.05$; Table 1). There was a significant group difference for age (One-way ANOVA: $F(1,118) = 3.32$, $p = 0.023$), where 9.0h and 5.0h groups in NFS3 were approximately 6-months younger than 6.5h and 5.0+1.5h groups in NFS4.

Design

Data are reported from the first half of NFS protocols that spanned 11-days (NFS3) and 15-days (NFS4). All groups were permitted 2 baseline nights (B_1-B_2) of the same 9.0h sleep opportunity, followed by a 3-day sleep restriction period (SR_1-SR_3) where groups diverged (Fig. 1), prior to the 4MT. For the 3 manipulation nights, the 9.0h group could sleep from

23:00-08:00, the 6.5h group from 12:15-06:45, and the 5.0h group from 01:00-06:00. The 5.0+1.5h group were permitted the same nocturnal TIB as the 5.0h group (01:00-06:00), but had an additional 1.5h TIB during a mid-afternoon nap (14:00-15:30). Participants were constantly monitored and were not permitted to sleep outside of these specified times.

Materials

Four Mountains Test

A 30 trial electronic version of the delayed match-to-sample task described previously[35], was programmed in E-Prime 2.0 (Psychology Software Tools, Inc, Sharpsburg, PA). Trials began with a 10-sec presentation of a sample landscape containing four mountains of varying shape, size and relative distance from each other, creating a unique topography (Fig. 2). Each landscape was rendered from a virtual camera in one of seven predefined viewpoints. This was followed by a 7-sec blank screen before presentation of a four-alternative choice of landscapes arranged in a 2x2 grid. The target image displayed the same landscape as the sample but from a different virtual camera position. Non-topographical features of images were also varied between sample and test images to ensure that task performance was based solely on topography. These included sunlight direction, cloud cover, atmospheric conditions and the color and texture of surfaces. The 3 foil images shared the same viewpoint and non-topographical features as the target, but the topography differed from the target in terms of shape, size and relative location of mountains. On screen position of targets and foils was randomized for each trial.

Participants selected landscape images with a keyboard press (‘Q’, ‘W’, ‘A’ or ‘S’). This highlighted the chosen image with a yellow box. Corrections before 20-secs were permitted.

The next trial began after 500ms. Trials were presented in a randomized single block lasting approximately 16-mins.

N-back Task

Both 1-back and 3-back tasks[44] were performed to establish that groups were matched for working memory and executive function at baseline, and during sleep restriction to contrast with 4MT performance. A letter appeared centrally for 1000ms, followed by a 3000ms blank screen inter-stimulus interval prior to presentation of the next letter. For the 1-back task, participants were required to respond with a button press to indicate whether the current stimulus matched (Y) or did not match (N) the letter in the previous trial. The 3-back task required participants to respond as to whether the current stimulus matched the letter presented 3-trials previously. The match to mismatch ratio was 8:24. Two performance indicators were measured: A' provided the participant's ability to discriminate between matches and mismatches (range: 0-1; chance performance = 0.5), while B" indicated their tendency towards liberal ($B"_D < 0$) or conservative ($B"_D > 0$) response bias.

Psychomotor Vigilance and Subjective Sleepiness

The psychomotor vigilance test (PVT)[45] provided an objective indication of sustained attention. Participants responded with the space bar when a counter appeared on screen, at random intervals between 2000ms and 10000ms. A beep alerted participants via headphones if no response was detected within 10000ms. This was performed in a 10-min continuous block. Response speed (1/RT) and lapses (responses slower than 500ms) were measured. The Karolinska Sleepiness Scale (KSS) provided an indication of subjective sleepiness.

Procedure

Participants' habitual term-time sleep was actigraphically assessed (Actiwatch AW-2, Philips Respironics, Inc., Pittsburgh, PA) for a one week period 1-3 months prior to the study (Table 1). One week prior to the study participants adhered to a sleep schedule (23:00-08:00), confirmed with actigraphy. The protocol took place during a school holiday period inside a boarding school in Singapore. Participants slept in twin-share bedrooms, while all testing and free time was strictly monitored in specified classrooms and common rooms throughout the 11-day and 15-day protocols. Breakfast (07:15-09:30), lunch (12:00-13:00), dinner (18:30-17:30) and snacks between meals were provided each day. Breakfast was delayed until 11:00 on B_2 and SR_3 in the 6.5h and 5.0+1.5h groups (NFS4) because of a glucose monitoring test that required a period of fasting (data not reported here).

Testing took place in a classroom with participants using individual laptops. Participants were sat approximately 1-metre apart across six perpendicular rows and were instructed not to look at other visible screens during task performance. Participants performed the n-back and PVT three times daily as part of a test battery on each day of the experiment. Timings varied by 30-mins between NFS3 and NFS4 studies. Analysis focused on the final baseline test battery (20:00 and 20:30) when participants had familiarized themselves with the tests, and on manipulation day SR_3 when the 4MT test took place. On day SR_3, the 9.0h and 5.0h groups from NFS3 performed the n-back task at 15:50, the PVT at 16:00, and the 4MT at 16:15. The 6.5h and 5.0+1.5h groups in NFS4 performed the same tasks 30-mins later: the n-back at 14:20, the PVT at 16:30, and the 4MT at 16:45. Participants were briefed altogether in each of the studies. They were shown four examples of the test stimuli and received feedback on the correct answers, as well as an explanation of why the foils were incorrect. Participants were instructed that each target image would be on screen for 10-sec, and that they should study the shape and arrangement of mountains carefully. They were

instructed to select the image which showed the same place as the target within 20-secs and could change their answer within that period.

Statistical Analysis

A one-way ANOVA and follow-up independent samples t-tests compared the four experimental groups, or Kruskal-Wallis H Test and Mann Whitney U Tests where Shapiro-Wilk indicated a non-normal distribution. Spearman's Rho correlations explored the relationship between 4MT performance and sleep features.

Polysomnography

Sleep was recorded using SOMNOtouch RESP portable devices (SOMNOmedics, GmbH, Germany) only for the NFS4 study (6.5h and 5.0h+1.5h groups). Recordings were performed on 3 nights (B_2, SR_1 and SR_3) and also the naps that followed on SR_1 and SR_3 in the 5.0+1.5h group. Electrodes were applied by trained technicians. EEG was recorded from 2 main channels (C3 and C4 according to the 10-20 system) referenced to the contralateral mastoids. The common ground and reference electrode were placed at Fpz and Cz. Left and right electromyogram and electrooculogram were also attached. Impedance <10KOhms was verified at each electrode. The sampling rate was 256Hz. Data was scored utilizing the Z3Score automated EEG system[46] and verified by a trained researcher. Prior research has linked post-nap cognitive performance with spindles[32] and SWS[33,47], therefore spindles and slow-wave activity (SWA) were analyzed at C3 referenced to A2. Slow (12-13.5Hz) and fast (13.5-15Hz) spindle density (spindles per minute) was assessed using an adapted automated algorithm[48]. Spectral analysis was performed on artefact-free non-overlapping 5-s epochs, focussing on SWA (0.6-4Hz) using a fast Fourier transform routine (Hamming window; 0.2Hz bin resolution). Total SWA was summed across all SWS epochs and

expressed as a percentage of total SWA in the baseline night (B2). As an exploratory analysis, total SWA in the first hour of nocturnal sleep was also computed as a marker of sleep pressure.

Results

Four Mountains Test

See Table 2 for a summary of all cognitive tests. A one-way ANOVA showed a significant main effect of group ($F(3,117) = 4.768$, $p = 0.004$). Follow-up t-tests revealed that relative to the 9.0h control group, the 5.0h group ($t(58) = 2.67$, $p = 0.01$; Cohen's $d = 0.69$), and the 6.5h group ($t(57) = 2.832$, $p = 0.007$; Cohen's $d = 0.74$) performed worse. In contrast, performance of the 5.0+1.5h group was not significantly different from the 9.0h control group ($t(57) = 0.055$, $p = 0.956$; Cohen's $d = 0.02$). Moreover, the 5.0+1.5h group performed significantly better than the 5.0h ($t(57) = 2.5$,$p = 0.015$; Cohen's $d = 0.65$) and 6.5h groups ($t(56) = 2.67$, $p = 0.01$; Cohen's $d = 0.7$). There was no significant difference between 5.0h and 6.5h groups ($t(57) = 0.205$,$p = 0.839$; Cohen's $d = 0.053$).

Thus, there was a similar performance deficit when obtaining 5.0h or 6.5h nocturnal TIB for 3 consecutive nights. However, if 6.5h TIB was split into 5.0h nocturnal TIB and a 1.5h TIB daytime nap (5.0+1.5h group), performance was comparable to the 9.0h controls.

We also examined the number of trials where no response was made (misses) as an indirect measure of attention. These were very low across the whole sample (M=1.5%, SD = 2.8%) and Kruskall-Wallis H-test showed no significant group differences ($\chi^2(3) = 1.042$, $p = 0.791$).

N-back Task

Prior to the sleep manipulation (B_2), there were no 1-back or 3-back group differences in A' ($p > 0.414$) and B''_D ($p > 0.230$). On SR_3, there were no significant group effects for 1-back A' ($\chi^2(3) = 3.77$, $p = 0.288$), and a trend for 3-back A' ($\chi^2(3) = 7.22$, $p = 0.065$). For response bias, groups did not differ for 1-back B''_D ($\chi^2(3) = 4.44$, $p = 0.218$), but there was a significant group effect for 3-back B''_D ($\chi^2(3) = 8.80$, $p = 0.032$). This appeared to be driven by the 5.0h+1.5h group who had a significantly more liberal response bias than the 5.0h group ($U = 258$, $p = 0.006$), while no other group comparisons yielded a significant difference ($p > 0.063$). This liberal bias of the 5.0+1.5h group may account for the trend of a group difference in 3-back A', where this group performed numerically better than the others (Table 2).

Next we correlated n-back performance on SR_3 with the 4MT within each group separately (16 comparisons). Only 3-back A' for the 5.0h group was significantly correlated with 4MT performance ($Rs = 0.398$, $p = 0.029$), although this did not survive FDR correction for multiple comparisons.

In sum, the split sleep schedule was associated with a shift in response bias for the more cognitively demanding 3-back task, but there were no significant group differences for accuracy and little indication of a relationship between n-back and 4MT performance. This suggests that unlike the 4MT, the 3-days of restricted sleep had relatively little impact on n-back performance. Together, these findings indicate that the sleep-related deficit observed in short-term topographical memory (4MT) was unlikely to reflect a more general impairment to working memory and executive function (n-back).

Psychomotor Vigilance and Subjective Sleepiness

At baseline (B_2), there were no significant group differences for PVT lapses, ($\chi^2(3) = 3.19$, p=0.363) or subjective sleepiness ($\chi^2(3) = 1.56$, p=0.669; Table 2). After the sleep manipulation however (SR_3), there was a significant main effect of group for lapses ($\chi^2(3) = 20.8$, p<0.001) and subjective sleepiness ($\chi^2(3) = 15.07$, p=0.002). Follow-up Mann Whitney U tests showed a similar pattern to the 4MT, whereby the 5.0+1.5h group had significantly fewer lapses (p<0.004) and less subjective sleepiness (p<0.033) than 6.5h and 5.0h groups. The 9.0h group also had fewer lapses than 6.5h and 5.0h groups (p<0.002), while subjective sleepiness was significantly lower than the 5.0h group (p=0.003) and trending to be lower than the 6.5h group (p=0.063). There were no significant differences for these measures between 9.0h and 5.0+1.5h groups (p>0.481), or between 6.5h and 5.0h groups (p>0.181).

Despite the similar pattern of results between PVT and 4MT at the group level, there were no significant correlations between PVT lapses or subjective sleepiness and 4MT performance within any group (p>0.081), indicating a dissociation within each participant between the effects of sleep restriction on attention, alertness and short-term topographical memory.

Actigraphy

In the screening period prior to inclusion in the study, participants showed a sleep pattern typical for Singaporean adolescents - shortened sleep on weekdays (TIB = 6.83 ± 0.94 hours, TST = 5.44 ± 0.84 [mean ± SD]) and sleep extension on weekends (TIB = 8.31 ± 1.00 hours, TST = 6.69 ± 0.96; Table 1). In the week prior to commencement of the study, participants adhered to a sleep schedule (23:00-08:00) confirmed with actigraphy (TIB = 8.9 ± 0.37, TST = 7.45 ± 0.53). Actigraphy during the study confirmed that our manipulation was

effective at reducing TST in each group (Table 3). Note that actigraphy using the manufacturer's default sensitivity settings underestimates adolescent TST by an average of ~30 minutes[49], therefore absolute values for TST should be interpreted with caution.

Polysomnography

Data was obtained for three of the four nights prior to the experimental day (B_2, SR_1, and SR_3), for the 6.5h and 5.0+1.5h groups (Fig. 4). Table 4 details nocturnal sleep, nap sleep and total sleep across each 24-hour period (i.e., nocturnal sleep and the following nap combined for the 5.0+1.5h group). There were no significant group differences in sleep macro-architecture during the baseline night (B_2) for any measure (TST, N1, N2, SWS, REM, $p > 0.05$; Fig. 4). The 5.0+1.5h group obtained significantly less TST than the 6.5h group on SR_1 ($p = 0.007$) and SR_3 ($p < 0.001$). This was due to increased sleep latency on both days ($p < 0.001$), because participants were required to fall asleep on two separate occasions, but wake after sleep onset (WASO) did not differ between groups ($p > 0.05$). This resulted in a reduction in total N2 on SR_1 ($p = 0.024$) and REM on SR_3 ($p = 0.011$), while SWS did not differ between groups at any point ($p > 0.05$).

Assessment of sleep characteristics in the SR_3 nap prior to the 4MT showed that performance was positively correlated with SWS duration ($R_s = 0.42$, $p = 0.023$) and total SWA (0.6-4Hz) ($r = 0.4$, $p = 0.03$). Other sleep stages and TST during the nap did not significantly correlate with 4MT performance ($p > 0.05$).

As a final exploratory analysis, we examined SWA in the first hour of nocturnal sleep on SR_3 as an indicator of the amount of accumulated sleep pressure. The 5.0+1.5h group (M=81.85%, SD=32.97) had significantly lower SWA than the 6.5h group (M=119.23%,

SD=53.12), t(52)=3.131, p=0.003, which suggests alleviation of sleep pressure by the nap under the split sleep schedule.

Discussion

We investigated how different sleep schedules affect a hippocampal-dependent test of short-term topographical memory. Performance was impaired after three nights of relatively mild nocturnal sleep restriction of 6.5h TIB, and was comparable to a more extreme schedule of sleep restriction (5h nocturnal TIB). In contrast, when sleep was split into 5h nocturnal sleep and a 1.5h daytime nap, performance was similar to a control group obtaining the recommended amount of sleep for adolescents[9] (9h nocturnal TIB).

The improved performance we observed after splitting sleep contrasts with prior research in adults, where overall performance was suggested to be determined by total sleep obtained within a 24-hour period, irrespective of whether sleep was split or not[24–26]. There is a wealth of research showing that a nap benefits cognition when it supplements a fixed amount of nocturnal sleep[32,33], but persons who napped in these studies obtained more sleep in the 24-hour period prior to testing. This makes it difficult to determine if the cognitive benefits stem from the additional sleep time or the distribution of sleep. The present split sleep design allows us to definitively attribute the benefit on memory to sleep distribution as total TIB was controlled.

The superior performance of students under the split sleep schedule (5.0+1.5h) is interesting given that total sleep time was less relative to the 6.5h nocturnal sleep group. This appears to simply be due to the fact that participants under the split sleep schedule were required to fall asleep twice. This results in a numerically longer sleep latency total that reduces total

sleep time given the fixed total sleep opportunity. Stage 2 and REM sleep duration were less under the split sleep schedule while SWS duration was unaffected. It is likely that the splitting of sleep afforded an additional opportunity to dissipate sleep pressure that built up by the mid-afternoon following hours of prior wakefulness. Evidence for such dissipation of sleep pressure comes from the finding of lower SWA in the first hour of nocturnal sleep in the split compared to 6.5h nocturnal sleep group. However, the mechanistic basis for why split sleep yields superior cognition under conditions of multi-night sleep restriction remains to be investigated in future studies.

Notwithstanding, participants who obtained more SWS and had greater slow wave activity in the nap prior to the 4MT performed better at the task. A relationship between hippocampal-dependent long-term memory operations and SWS has been consistently observed[33,50], and here we show a similar relationship for a hippocampal-dependent short term memory task. These findings are consistent with the idea that SWS benefits cognitive function, perhaps through the downscaling of synapses potentiated during extended wakefulness. This could renew the capacity of networks to encode new information[34] and may account for the enhanced ability of the split sleep group to encode and manipulate scenes in the 4MT.

The impairment to 4MT performance after only 3-nights of 6.5h TIB contrasts with the lack of a significant effect on n-back performance. The latter finding agrees with prior studies where several nights of sleep restriction did not affect WM and executive function[16–18]. In adolescents, n-back performance decrements only emerged after 4-nights of 5h TIB[7]. One study utilised a visuospatial working memory task that required the maintenance and manipulation of a visual image[19], but did not depend on the allocentric spatial processing that is critical to performance of the 4MT[35]. They found that 3-weeks of 6.5h TIB per 28h period led to deficits in speed but not accuracy of this task[19]. Taken together, these findings

suggest that allocentric spatial processing may be more vulnerable to sleep restriction than working memory.

Deficits to WM and executive function after a night of sleep deprivation are strongly linked to impaired prefrontal function[11–13]. While the 4MT tests a form of WM, it is thought to provide a sensitive index of hippocampal-dependent spatial processing[35–40], and neuropsychological evidence suggests it is less affected by prefrontal damage[39]. Speculatively, the high sensitivity of the 4MT to sleep restriction suggests that hippocampal function is particularly sensitive to chronic sleep loss. The current study did not measure brain activity during performance, and to our knowledge the only imaging studies of WM have examined total sleep deprivation rather than partial sleep restriction[11,13], therefore further work is necessary to uncover the neurophysiological correlates of these impairments.

The sensitivity of the 4MT to multiple nights of sleep restriction is congruent with observations of impaired episodic memory encoding after sleep loss and associated hippocampal dysfunction. A single night of sleep deprivation[42,43] or 5 consecutive nights of only 5-hours TIB[6] significantly reduced the capacity to encode new information, possibly as a result of reduced hippocampal activity during encoding[43] as well as reduced capacity for long-term potentiation in the hippocampus[51,52]. We show that a less severe and relatively common form of chronic sleep restriction (6.5h on 3 consecutive nights) can also impair hippocampal dependent cognition.

The pattern of results for psychomotor vigilance and subjective sleepiness were similar to the 4MT, but no significant correlations between the tasks were observed. This indicates that within individual participants, capability in one cognitive domain was not associated with their

ability in another. Similar dissociations between cognitive measures have been noted several times in prior work: between subjective and objective measures of sleep loss[53], as well as vigilance and memory[6,43]. The long trials of the 4MT (10 sec to encode, 20 sec to make a response) make it unlikely that lapses in concentration associated with the PVT would impact on performance, supported by the low number of missed trials on the 4MT. Moreover, the rapid presentation of the n-back task makes it arguably more vulnerable to attentional lapses, and yet, it was not affected after 3 nights of sleep restriction. To summarize, while decline in vigilance after sleep deprivation is a robust observation[6–8,10], it is unlikely to account for the short-term topographical memory effects we observed.

Several limitations to the present study should be kept in mind. While the split sleep group appeared to perform as well as controls, the sleep they obtained was far below the recommended 9.0h for this age group[9], therefore we do not advocate for students to keep this type of chronically restricted sleep schedule. Not only are there myriad other negative health consequences associated with insufficient sleep[2], but our observations may also be conditional on the time at which participants were tested. The 4MT took place at 16:45, 1.5h after the nap, and it is unclear if performance would differ at other times of day and other times relative to the time at which the nap took place. Sleepiness and sustained attention have been shown to be enhanced by a nap for a limited window only[29] and this may also be the case for the 4MT. Our prior study also suggests that morning 4MT performance would be likely reduced: a 1h nap enhanced afternoon PVT performance in adolescents under a 5h TIB nocturnal sleep schedule, but morning performance was similarly impaired to a no-nap condition[8]. The 4MT was only tested once in the current study in order to limit the effects of training and memory consolidation between sessions, therefore other times of day could be tested in future studies to provide a more complete picture of performance under a split sleep schedule. It may also be useful to examine the change in performance between

baseline and sleep restriction tests in order to assess the impact of different sleep schedules at the individual level.

In sum, hippocampal-dependent topographical memory appears to be negatively affected by even three nights of relatively mild sleep restriction, but this deficit is recovered when sleep is split across a nocturnal period and a daytime nap. This suggests that under conditions of chronic sleep restriction, a split sleep schedule may optimize the cognitive and neurophysiological functions that underpin some aspects of learning.

Abbreviations

4MT – Four Mountains Test

N1 – Stage 1 sleep

N2 – Stage 2 sleep

SWS – Slow Wave Sleep

REM – Rapid-Eye Movement Sleep

NREM – Non Rapid-Eye Movement Sleep

SWA – Slow Wave Activity

TIB – Time-In-Bed

TST – Total-Sleep-Time

PSG – Polysomnography

EEG – Electroencephalography

NFS3 – Need For Sleep Study 3

NFS4 – Need for Sleep Study 4

BMI – Body Mass Index

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Figure 1. Protocol. *Each of the 4 groups received 9.0h nocturnal TIB for 2 nights prior to a 3-day manipulation period. These groups subsequently had: 9.0h nocturnal TIB (23:00-08:00), 6.5h nocturnal TIB (12:15-06:45), 5.0h nocturnal TIB (01:00-06:00) with a 1.5h TIB daytime nap opportunity (14:00-15:30), or 5.0h nocturnal TIB (01:00-06:00). On the second baseline day (B2), several measures from an evening test battery (KSS, N-back, and PVT) were analyzed to establish that groups did not differ prior to the sleep manipulation. The Four Mountains Test took place at 16:45 on the third manipulation day (SR_3), after the KSS, N-back and PVT. Note that stated times on SR_3 refer to the 6.5h and 5.0+1.5h groups (NFS4 study), while tests were consistently 30-mins earlier for the 9h and 5.0h groups (NFS3 study).*

For the 3 manipulation nights, the 9.0h group could sleep from 23:00-08:00, the 6.5h group from 12:15-06:45, and the 5.0h group from 01:00-06:00. The 5.0+1.5h group were permitted the same nocturnal TIB as the 5.0h group (01:00-06:00), but had an additional 1.5h TIB during a mid-afternoon nap (14:00-15:30).

Figure 2. The Four Mountains Test. *Participants viewed a landscape containing four mountains. After a delay, they had to identify the same place from an alternative viewpoint (highlighted in yellow) from 3 distractor scenes.*

Figure 3. Behavioural results and sleep correlation. *(a) There was significantly lower performance in the 5.0h and 6.5h groups relative to the 9.0h control group. By contrast, there was no impairment to performance when 6.5h TIB was split across nocturnal sleep and a daytime nap (5.0+1.5h group). (b) Duration of SWS during the nap prior to the task was significantly correlated with 4MT performance. Error bars represent standard error of the mean (SEM).*

Figure 4. Sleep parameters prior to the 4MT. *Graphs represent combined sleep characteristics over each 24-h period. (a) The 5.0+1.5h group obtained significantly less total sleep time than the 6.5h group during the sleep restriction period (SR1-SR3). (b) Underlying this difference was significantly less stage 2 sleep on SR1 and (d) less REM sleep on SR3. (c) Slow-wave sleep did not differ between groups at any point. Error bars represent SEM.*

Figure 1

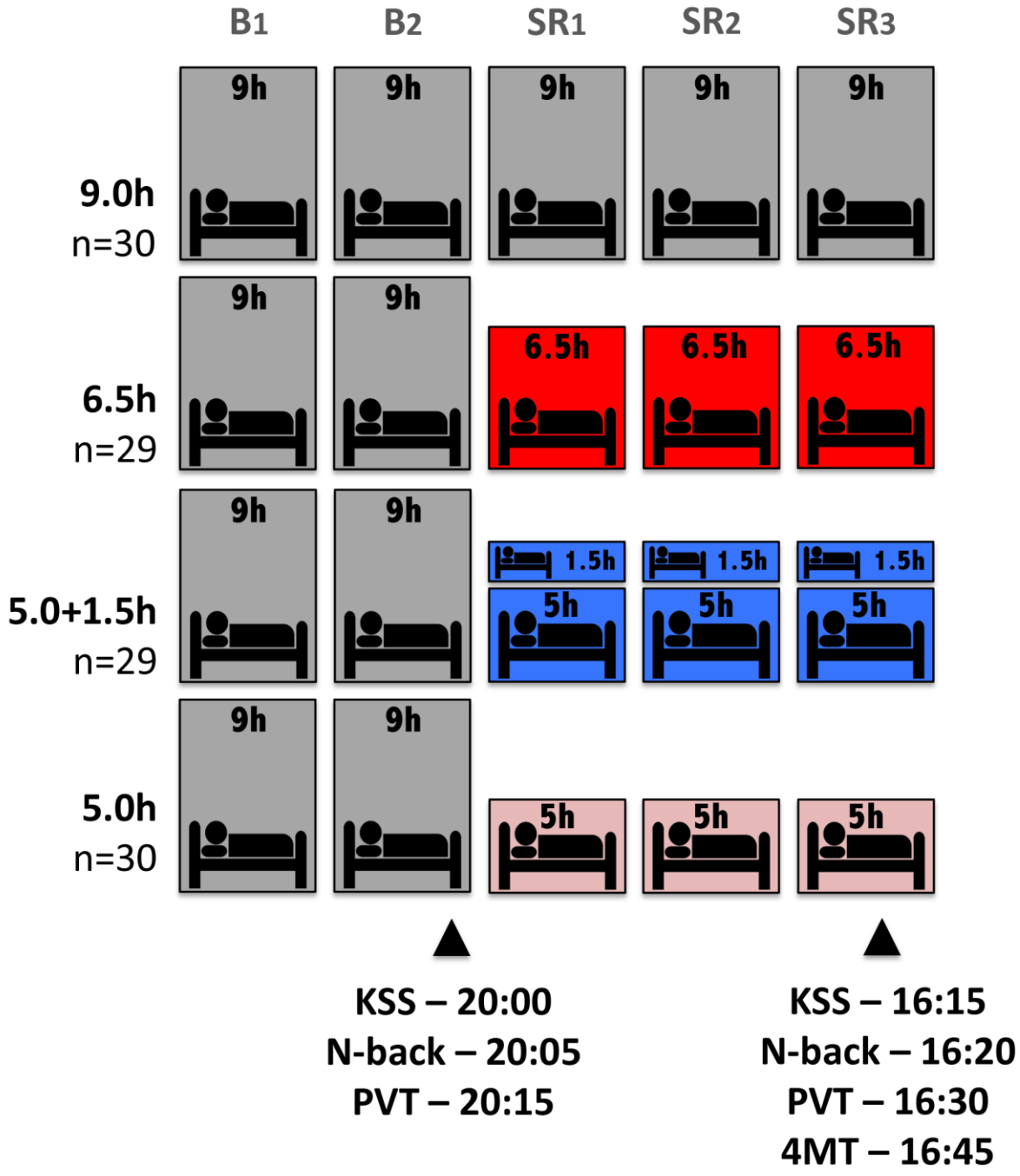

Figure 2

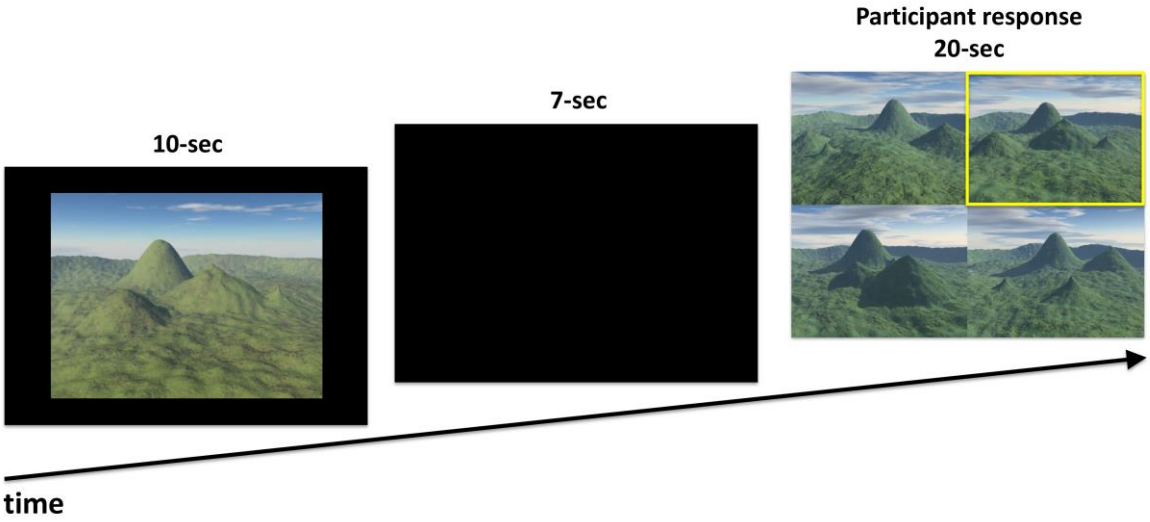

Figure 3

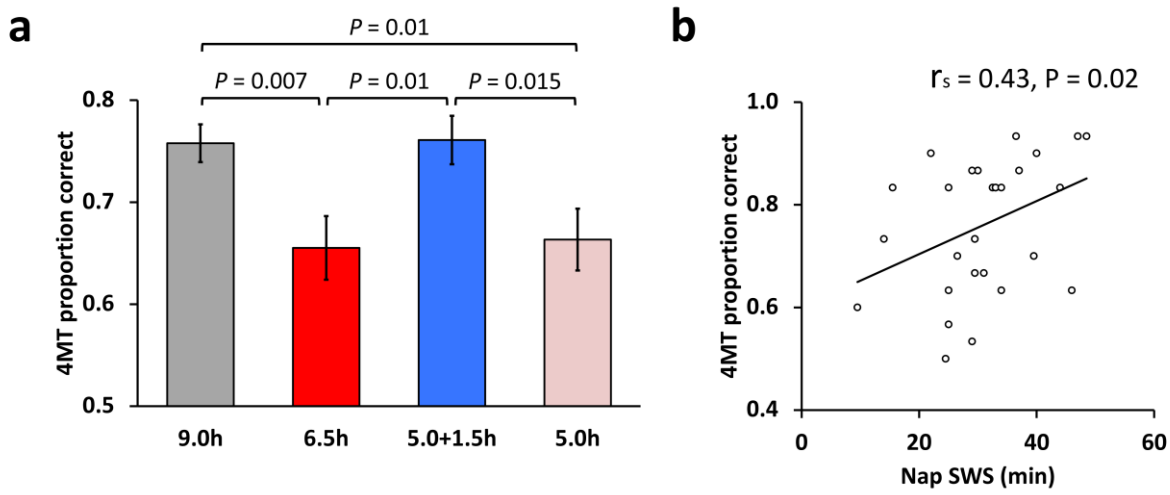

Figure 4

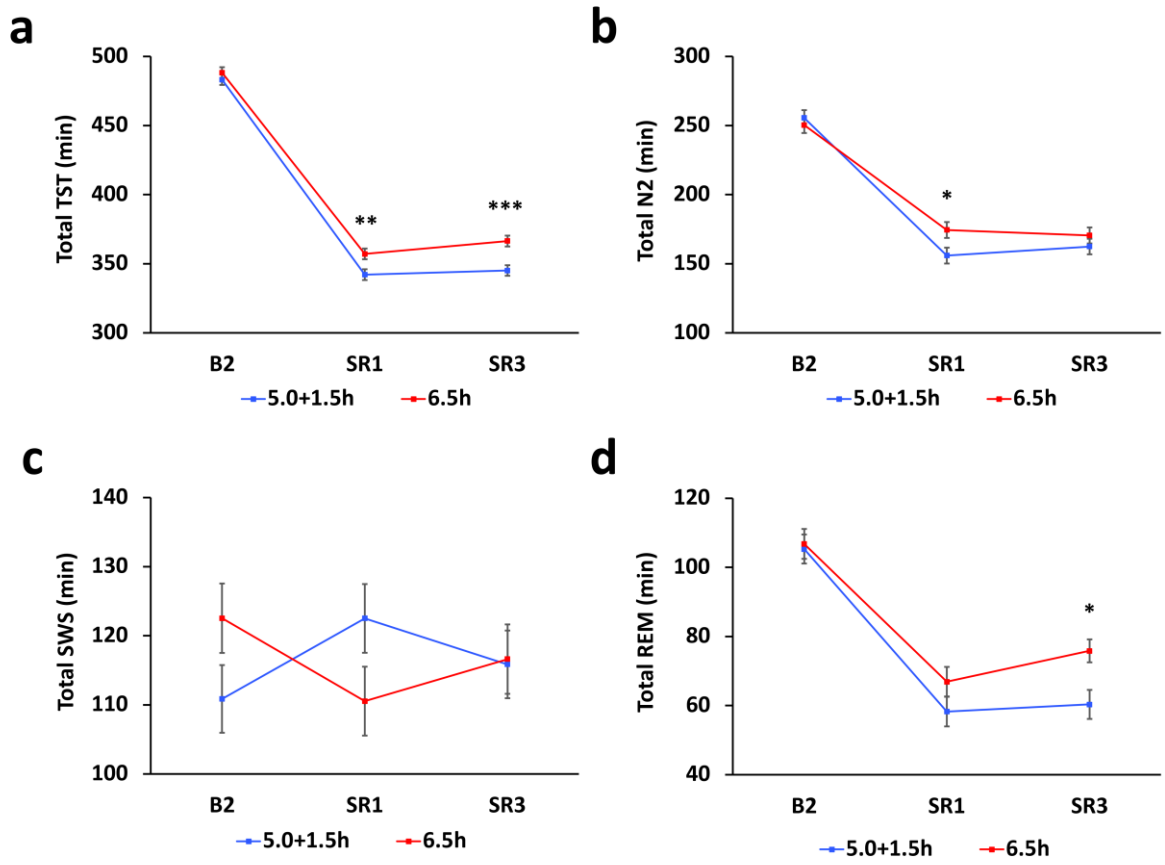

Table 1. Screening characteristics.

	9.0h		6.5h		5.0+1.5h		5.0h		F/χ^2	p
	Mean	SD	Mean	SD	Mean	SD	Mean	SD		
n	30	-	29	-	29	-	30	-	-	-
Age (y)	16.1	0.6	16.6	1.1	16.6	0.7	16.1	0.6	3.32	.023*
Gender (number of males)	15	-	15	-	15	-	15	-	0.08	.972
Caffeinated drinks per day	0.4	0.5	0.6	0.8	0.6	0.7	0.5	0.8	0.76	.517
Body mass index	20.0	3.5	21.3	3.5	20.7	2.8	20.3	3.3	0.91	.437
Raven's Advanced Progressive Matrices score	8.8	1.9	8.8	1.9	9.2	1.6	8.8	1.5	0.29	.834
Beck Anxiety Inventory score	8.0	5.5	9.3	6.7	10.4	6.3	9.4	6.9	0.60	.618
Beck Depression Inventory score	8.6	5.8	11.0	5.3	9.2	5.5	9.3	6.3	0.79	.501
Morningness-Eveningness Questionnaire score	53.3	6.4	49.0	7.5	50.7	7.1	52.1	8.4	1.71	.169
Epworth Sleepiness Scale score	6.7	2.8	8.2	3.4	7.9	3.8	7.0	3.4	1.35	.262
Chronic Sleep Reduction Questionnaire										
Total score	35.2	5.3	35.2	6.0	36.1	4.7	35.0	5.1	0.23	.879
Shortness of sleep	13.1	2.2	12.7	2.1	13.0	2.0	13.1	2.2	0.25	.864

Irritation	6.4	1.7	6.4	1.5	6.8	1.9	6.9	2.3	0.58	.631
Loss of energy	8.1	2.2	8.5	2.1	8.0	2.0	7.5	1.5	1.19	.319
Sleepiness	7.6	1.6	7.7	2.3	8.3	1.5	7.5	1.8	1.08	.362
Pittsburgh Sleep Quality Index global score	4.7	2.1	4.5	1.5	4.2	1.8	4.6	1.5	0.32	.815
Actigraphy										
TIB on weekdays (h)	6.6	1.0	7.0	0.8	6.8	1.1	6.7	0.8	0.74	.533
TIB on weekends (h)	8.3	1.0	8.5	1.1	8.2	1.1	8.4	0.8	0.49	.690
TIB on average (h)	7.2	0.8	7.4	0.6	7.2	0.9	7.4	0.7	0.86	.462
TST on weekdays (h)	5.4	0.9	5.5	0.8	5.5	0.9	5.4	0.8	0.24	.870
TST on weekends (h)	6.8	0.9	6.8	1.1	6.6	1.0	6.6	0.8	0.33	.804
TST on average (h)	5.8	0.7	5.9	0.7	5.8	0.7	5.8	0.8	0.27	.849
Sleep efficiency (%)	81.6	6.2	79.0	5.6	81.0	6.6	78.8	7.1	1.67	.178

Note. y = year; SD = standard deviation; TIB = time in bed; TST = total sleep time; h = hour; actigraphy threshold: medium

* $p < .05$

Table 2. Performance for all cognitive tests.

	9.0h		6.5h		5.0+1.5h		5.0h		F/χ^2	p
	Mean	SD	Mean	SD	Mean	SD	Mean	SD		
Baseline - B2										
PVT lapses	2.60	3.15	3.21	4.97	2.24	2.63	4.63	5.51	3.19	.363
KSS	4.47	1.48	4.67	1.41	4.79	1.46	4.86	1.38	1.56	.669
1-back A’	0.97	0.03	0.96	0.06	0.98	0.02	0.97	0.03	2.85	.415
1-back B”	0.12	0.63	0.33	0.63	0.02	0.71	0.32	0.70	4.30	.231
3-back A’	0.93	0.05	0.90	0.08	0.92	0.06	0.91	0.08	2.46	.483
3-back B”	0.27	0.68	0.33	0.69	0.18	0.75	0.34	0.74	1.50	.681
Sleep restriction - SR3										
PVT lapses	2.93	4.62	11.45	14.02	2.90	3.57	8.48	9.98	20.80	.000**
KSS	4.53	1.80	5.28	1.75	4.50	1.32	5.87	1.59	15.07	.002**
1-back A’	0.95	0.04	0.96	0.06	0.96	0.06	0.96	0.05	3.77	.288
1-back B”	0.34	0.76	0.15	0.73	0.11	0.74	0.41	0.70	4.44	.218
3-back A’	0.90	0.18	0.91	0.10	0.95	0.05	0.89	0.94	7.22	.065

3-back B”	0.15	0.72	0.17	0.71	-0.20	0.83	0.41	0.71	8.80	.032*
4MT (proportion correct)	0.76	0.10	0.66	0.16	0.76	0.13	0.66	0.16	4.77	.004**

Note. SD = Standard Deviation; PVT = Psychomotor Vigilance Test; KSS = Karolinska Sleepiness Scale; 4MT = Four Mountains Test; h = hour; * $p < .05$; ** $p < .01$

Table 3. Total sleep time across baseline and manipulation nights (assessed with actigraphy)

	9h		6.5h		5.0+1.5h		5h	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Baseline Nocturnal (B_1- B_2)								
TST	453.6	32.6	453.8	42.0	455.1	33.2	456.8	30.6
Manipulation Nocturnal (SR_1- SR_3)								
TST	446.7	30.0	326.4	29.0	246.5	20.9	259.9	17.1
Manipulation Nap (SR_1- SR_3)								
TST	-	-	-	-	72.9	8.7	-	-

Note. SD = standard deviation; TST = total sleep time (min); actigraphy threshold: medium

Table 4. Sleep architecture of the 6.5h and 5.0+1.5h groups during baseline and manipulation nights, measured with polysomnography.

		5.0+1.5h		6.5h			
		Mean	SD	Mean	SD	*t*	*p*
B2	Nocturnal						
	N1	11.5	7. 8	8.6	6.1	1.54	.130
	N2	255.5	31.1	251.3	37.6	.46	.650
	SWS	110.9	22.2	121.2	31.6	-1.43	.158
	REM	105.3	20.3	106.6	22.0	-.224	.824
	TST	483.2	27.1	487.8	26.6	-.634	.529
	N2 Latency	36.9	18.5	30.6	12.3	1.494	.140
	WASO	20.4	19.5	22.2	20.1	-.341	.735
	Sleep Efficiency	89.5	5.0	90.3	4.9	-.589	.559
SR1	Nocturnal						
	N1	3.6	3.0	5.3	3.5	-1.88	.065
	N2	124.5	21.0	174.4	32.6	-6.72	.000*
	SWS	94.7	17.1	110.5	33.0	-2.25	.030*

REM	48.5	18.7	66.9	18.5	-3.68	.001*
TST	271.3	16.4	357.1	14.3	-20.67	.000*
N2 Latency	22.9	14.4	23.1	10.3	-.075	.941
WASO	6.4	10.8	10.3	9.9	-1.38	.172
Sleep Efficiency	90.4	5.6	91.6	3.7	-.938	.352
Nap						
N1	1.8	1.8	-	-	-	-
N2	31.2	12.0	-	-	-	-
SWS	27.8	13.0	-	-	-	-
REM	10.1	10.2	-	-	-	-
TST	70.9	15.7	-	-	-	-
N2 Latency	13.9	8.2	-	-	-	-
WASO	5.7	12.1	-	-	-	-
Sleep Efficiency	78.7	17.4	-	-	-	-
Total						

	N1	5.5	3.8	5.3	3.5	.25	.802
	N2	156.8	25.3	174.4	32.6	-2.23	.030*
	SWS	122.2	23.1	110.5	33.0	1.51	.136
	REM	58.1	25.2	66.9	18.5	-1.49	.144
	TST	342.6	28.2	357.1	14.3	-2.39	.022*
	N2 Latency	36.8	19.3	23.1	10.3	3.26	.002*
	WASO	11.7	17.2	10.3	9.9	.381	.705
	Sleep Efficiency	87.8	7.3	91.6	3.7	-2.42	.019*
SR3	Nocturnal						
	N1	4.5	6.6	3.7	3.2	.58	.563
	N2	125.8	22.2	170.2	26.7	-6.79	.000*
	SWS	84.8	16.4	116.2	23.3	-5.87	.000*
	REM	50.6	14.6	76.5	21.1	-5.38	.000*
	TST	265.7	17.1	366.6	9.2	-27.75	.000*
	N2 Latency	29.6	16.1	17.1	8.9	3.55	.000*
	WASO	5.3	7.7	6.8	6.2	-.778	.440

Sleep Efficiency	88.5	5.7	94.0	2.4	-4.59	.000*
Nap						
N1	2.0	1.4	-	-	-	-
N2	36.7	12.3	-	-	-	-
SWS	31.0	9.4	-	-	-	-
REM	9.8	8.4	-	-	-	-
TST	79.5	3.9	-	-	-	-
N2 Latency	9.7	3.9	-	-	-	-
WASO	1.4	1.4	-	-	-	-
Sleep Efficiency	88.2	4.4	-	-	-	-
Total						
N1	6.5	7.1	3.7	3.2	1.86	.068
N2	162.5	26.1	170.2	26.7	-1.10	.276
SWS	115.9	21.2	116.2	23.3	-.061	.952
REM	60.3	17.7	76.5	21.1	-3.11	.003*

TST	345.1	18.6	366.6	9.2	-5.53	.000*
N2 Latency	39.3	18.1	17.1	8.9	5.74	.000*
WASO	6.7	8.0	6.8	6.2	-.037	.971
Sleep Efficiency	88.5	4.8	94.0	2.4	-5.41	.000*

Note. SD = standard deviation; N1 = stage 1 sleep (min); N2 = stage 2 sleep (min); SWS = slow-wave sleep (min); REM = rapid-eye movement sleep (min); TST = total sleep time (min); N2 latency = time to first epoch of stage 2 sleep (min); WASO = wake after sleep onset (min); SE = sleep efficiency (% TIB) * $p <$ .05