Overnight Sleep Enhances Hippocampus-Dependent Aspects of Spatial Memory

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Study Objectives: Several studies have now demonstrated that spatial information is processed during sleep, and that posttraining sleep is beneficial for human navigation. However, it remains unclear whether the effects of sleep are primarily due to consolidation of cognitive maps, or alternatively, whether sleep might also affect nonhippocampal aspects of navigation (e.g., speed of motion) involved in moving through a virtual environment.

Design: Participants were trained on a virtual maze navigation task (VMT) and then given a memory test following either a day of wakefulness or a night of sleep. Subjects reported to the laboratory for training at either 10:00am or 10:00pm, depending on randomly assigned condition, and were tested 11 h later. Overnight subjects slept in the laboratory with polysomnography.

Setting: A hospital-based academic sleep laboratory.

Patients or Participants: Thirty healthy college student volunteers.

Interventions: N/A.

Measurements and Results: Point-by-point position data were collected from the VMT. Analysis of the movement data revealed a sleep-dependent improvement in maze completion time ($P < 0.001$) due to improved spatial understanding of the maze layout, which led to a shortening of path from start to finish ($P = 0.01$) rather than faster exploration speed through the maze ($P = 0.7$).

Conclusions: We found that overnight sleep benefitted performance, not because subjects moved faster through the maze, but because they were more accurate in navigating to the goal. These findings suggest that sleep enhances participants' knowledge of the spatial layout of the maze, contributing to the consolidation of hippocampus-dependent spatial information.

Keywords: consolidation, EEG, learning, maze, procedural, speed

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INTRODUCTION

Sleep is beneficial for human memory across a wide variety of domains, including verbal learning,[1,2] motor skill acquisition,[3,4] and emotional memory.[5,6] The effect of sleep on human spatial memory has received relatively less attention, which is surprising because much of what is known about the neural basis of sleep-dependent memory consolidation comes from studies of spatial navigation in animals. Seminal rodent studies, some dating back more than 2 decades, show that patterns of hippocampal place cell activity established during waking spatial navigation are later reactivated during nonrapid eye movement sleep (NREM).[7-10] This reinstatement of experience-dependent neural activity during sleep is thought to be critical to memory consolidation, allowing fragile new memory traces to become increasingly stabilized and reorganized over time.[11-13]

In recent years, human studies of spatial navigation have been facilitated by the advent of low-cost software platforms for implementing "virtual" spatial environments. Meier-Koll et al.[14] first suggested a role for sleep in consolidating such spatial learning, observing that training in computerized maze environments increases spindles during subsequent stage 2 sleep. Later, Peigneux et al.[15] elegantly demonstrated that hippocampal activity during postlearning sleep increases after training and predicts overnight improvement on a virtual environment navigation task, consistent with the notion that "reactivation" of spatial learning occurs during sleep in humans. Yet it remains unclear whether sleep actually provides a performance benefit on spatial navigation tasks. Subsequent imaging studies using a similar virtual environment showed that, although sleep resulted in a functional reorganization of networks supporting navigation, this was not beneficial for memory performance.[16,17] On a variety of speed and accuracy measures (including distance traveled, distance remaining to the goal at the end of a trial, speed of movement, time spent hesitating, and recognition of landmarks), participants who were sleep deprived following encoding showed no impairment of performance, relative to those who obtained a full night of sleep.[16,17] It was concluded that, although sleep reorganizes the representation of spatial memory in the brain, this is not manifested in a performance benefit.[16,17]

In contrast, several other studies have suggested that sleep does enhance memory for spatial environments. Ferrara et al.[18] found that after participants walked on a route through an actual city, sleep facilitated correct recognition of sequences of landmarks that they had encountered. Later studies of virtual navigation tasks[19-21] showed that the amount of time required for participants to navigate to goals within an environment is significantly decreased across a retention interval filled with sleep, but not across equivalent periods of wakefulness. To minimize procedural learning, these studies allowed participants extensive practice prior to sleep, hoping to test the effect of sleep on the hippocampus-dependent formation of spatial maps, rather than on the improvement of procedural skills related to using a keyboard to navigate through virtual space. However, in all
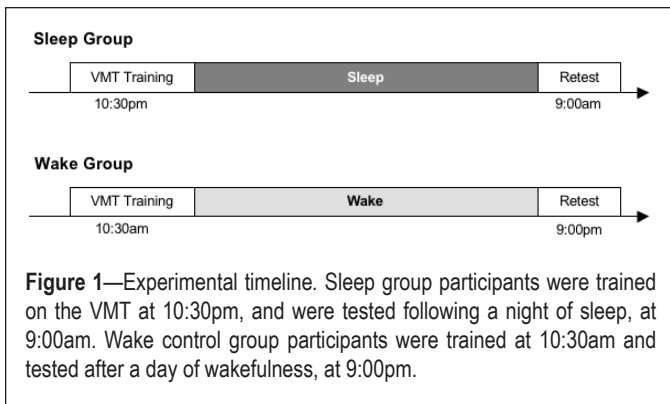
Figure 1—Experimental timeline. Sleep group participants were trained on the VMT at 10:30pm, and were tested following a night of sleep, at 9:00am. Wake control group participants were trained at 10:30am and tested after a day of wakefulness, at 9:00pm.

cases, the effect of sleep was measured exclusively as reduction in the time taken to reach a particular goal or landmark.[19-21]

However, measures of "completion time" alone cannot distinguish between the accuracy of a path taken from start to finish and the speed with which a subject moves through an environment. The time that a participant takes to navigate between two points in a virtual environment is influenced by the accuracy of his or her route, by the speed of his or her movement, and by the number and duration of deliberative pauses. For example, subjects who have not formed a strong spatial cognitive map of the environment might compensate by moving faster through the environment. Alternatively, a subject with a strong cognitive map may make more deliberative pauses en route to the goal. In a recent study of memory in post-traumatic stress disorder, Tempesta et al.[22] measured overnight changes in virtual navigation accuracy by determining the number of trials on which participants chose the "optimal" route to the goal. However, because there were no waking control groups in this study, the effect of sleep relative to wakefulness was not determined.

Thus, although suggestive, the literature remains contradictory and incomplete. Two studies using accuracy-based performance measures have failed to find an effect of sleep on navigation performance.[16,17] Other research has shown that sleep shortens the time needed for participants to navigate to a goal,[18,19,21,23] but because completion time is influenced both by accuracy and speed of navigation, we cannot yet definitively conclude that sleep enhances the accuracy of human hippocampus-dependent spatial maps. In the current study, to determine whether sleep specifically consolidates the hippocampus-dependent spatial aspects of navigation (i.e., formation of a cognitive map), we revised our virtual maze navigation task (VMT)[21,23] to generate multiple performance metrics that not only track the speed with which participants navigate the maze, but also the moment-by-moment path taken by the subject from start to finish. Examining the effect of sleep on multiple dependent measures, we expected to find that sleep would selectively enhance performance on measures of navigation accuracy, but have no effect on the speed of movement through the environment.

MATERIALS AND METHODS

Participants

Thirty-six Boston-area college students enrolled in the study. Participants reported being free from psychiatric and sleep disorders, and were instructed to abstain from caffeine, alcohol, and drug use for 24 h prior to the study. Participants were also instructed to maintain a regular sleep schedule on the nights preceding the study, and filled out a 3-day retrospective sleep log describing their recent sleep behavior.

In past studies using our VMT, we found that subjects with little or no prior experience playing three dimensional (3D)-style video games performed very poorly on the task and failed to show sleep-dependent improvement.[21] Participants with limited video game experience also experienced high rates of "cybersickness"[24] induced by the task. Thus, participants were screened for prior game experience by asking about the typical frequency with which they play 3D-style/first person perspective games. Those reporting playing such games less than once per year were excluded from participation.

Six participants were excluded from analysis: one participant in the wake group napped during the day, two participants' sleep data were lost due to equipment malfunction, and three participants failed to adequately perform the task as indicated by failure to find the maze exit on two or more trials at training. This resulted in a final sample of n = 30 (19 female and 11 male, age 19.6 ± 2.0 years), n = 21 in the two sleep groups (see next paragraphs), and n = 9 in the wake control group. Sleep and wake group participants were equivalent in terms of prestudy bedtime and prestudy total sleep time. At baseline, there were no significant differences between sleep and wake group participants in Epworth Sleepiness Scale scores (ESS), Stanford Sleepiness Scale (SSS) ratings, or subjective ratings of task difficulty and engagement.

Procedures

Changes in spatial memory across a retention interval filled with sleep were compared to those across an equivalent period of wakefulness. Participants were pseudorandomly assigned to either the sleep group (n = 11), sleep + awakenings group (n = 10), or wake group (n = 9). Following our prior work, a secondary study goal was to examine whether dreaming of the learning task was related to memory performance. Thus, the sleep + awakenings group was interrupted during the night to collect reports of dream experience (see next paragraphs). The separate sleep group, without awakenings, served to eliminate concern over possible effects of the dream reporting procedure on sleep-dependent memory consolidation.

The experimental timeline is illustrated in Figure 1. In the sleep groups, participants reported to the laboratory at 9:00pm where they gave written consent and completed a demographic questionnaire, a 3-day retrospective sleep log, and the Epworth Sleepiness Scale.[25] Participants were then wired for polysomnographic (PSG) recording. Throughout the night, electroencephalography (EEG), electrooculography (EOG), and electromyography (EMG) data were acquired. Just prior to beginning training on the VMT at 10:30pm (see next paragraphs), participants rated subjective alertness using the SSS.[26] Immediately following training, participants provided subjective ratings of task difficulty and engagement on visual analog scales, and were then given an 8-h sleep opportunity. Retesting on the VMT began a minimum of 30 min after awakening in the morning, at approximately 9:00am.

Wake group participants completed the identical protocol, except that they reported to the laboratory at 10:00am, and were retested that evening at 9:00pm. After giving written con-

sent and completing questionnaires identical to the sleep group, wake group participants underwent training on the VMT beginning at 10:30am, and were then allowed to leave the laboratory and go about their normal day, with prohibitions on caffeine, alcohol consumption, and napping. Participants returned to the laboratory for retesting at 9:00pm (see Figure 1).

The protocol for participants in the sleep + awakenings group was identical to that for the sleep group except that they were awakened several times during the night to report dream experiences. The purpose of this procedure was to assess relationships between sleep-dependent performance improvement and the content of subjective experience.[20] Up to 10 sleep onset dream reports were collected during the first hour of the night, 30, 60, or 90 sec after sleep onset (latencies following a randomized order). Three additional reports were collected from stage 2 NREM sleep later in the night, and a final report was given in the morning. However, only one participant reported a dream experience clearly related to the VMT, precluding useful analysis of this data. Sleep + awakenings and sleep group participants did not differ significantly on any measure of maze performance. Data from these groups were therefore combined for all analyses reported in the main text. Results for each sleep group are reported separately in the supplemental material.

Sleep and sleep + awakenings group participants did exhibit minor differences in sleep architecture, with the sleep + awakenings group having less total sleep time, particularly in stage 2 and REM sleep (see supplemental material). However, as described in the Results section, these aspects of sleep architecture were unrelated to task performance in both groups, as well as in the combined group. Participants in the two sleep groups exhibited equivalent alertness in the morning, as measured by the SSS.

Virtual Maze Task

The VMT[21,23] (Figure 2) used in previous studies from our laboratory was redesigned to permit separate examination of the distance, speed, and amount of backtracking during maze navigation. Constructed using the Unreal Tournament 3 Editor (Epic Games, Cary, NC), the task was implemented on a personal computer and projected on the wall of a darkened testing room, resulting in a 60″ × 44″ (28° × 20°) viewing area. A modified USB number pad with four keys allowed forward and backward movement, as well as left and right turns. The maze layout was identical to that used in our previous studies, and completion times were comparable to those obtained with previous versions of the task.[21,23]

The training session began with a practice period. On screen, the participants began by facing the maze exit, depicted as a glowing door, and had 5 min to explore the maze with the instruction that "after this exploration period, you will then be asked to navigate to the exit door from different starting points within the maze." This exploration period was followed by a series of three training trials in which participants attempted to find the maze exit as quickly as possible. As in previous studies, salient objects served as landmarks. Fog diminished visibility within the maze linearly with virtual distance from the player, forcing the participants to rely on proximal visual information for navigation rather than visual cues in the distance. For each trial, participants began at a unique starting point, each equidis-
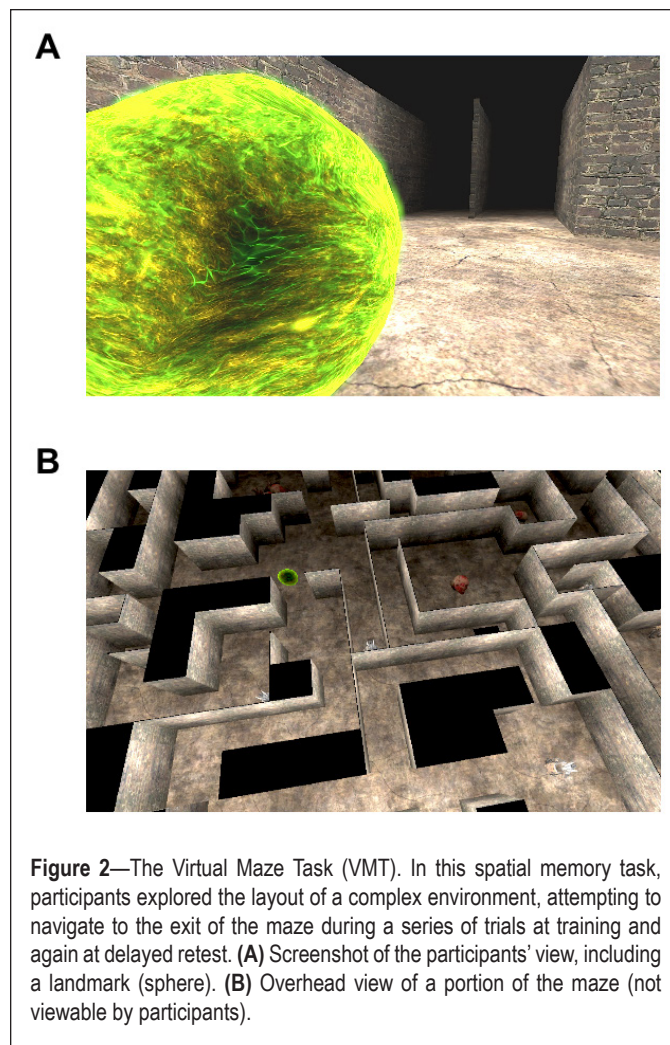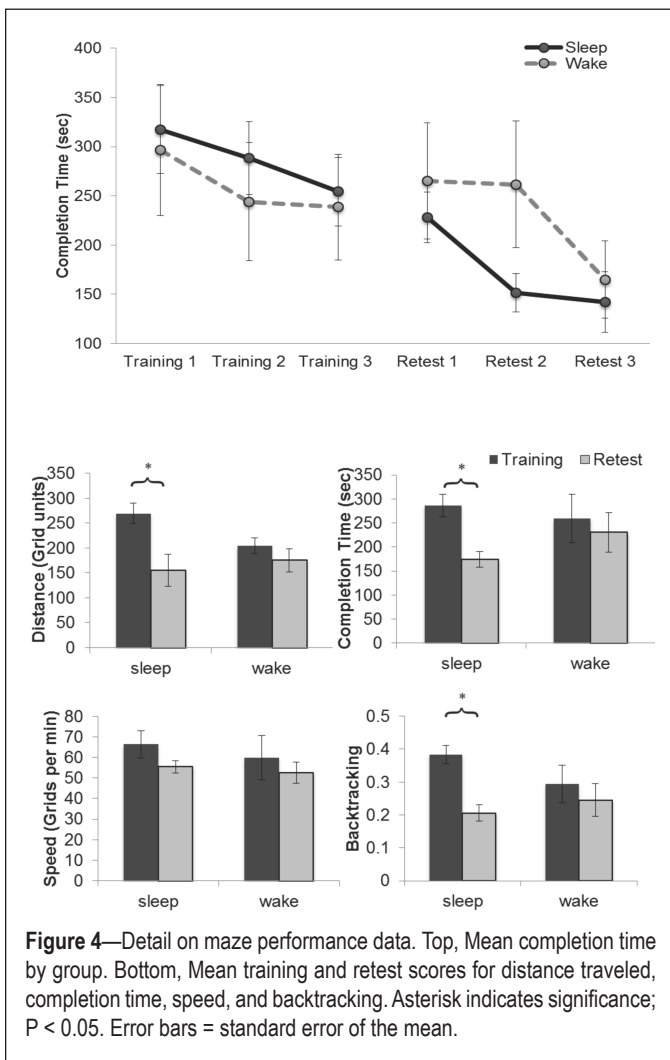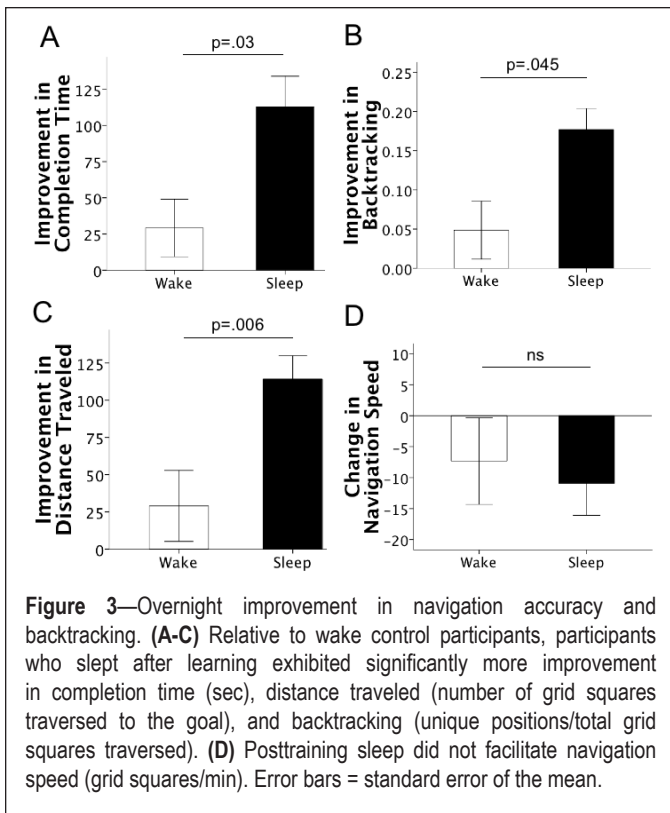

Figure 2—The Virtual Maze Task (VMT). In this spatial memory task, participants explored the layout of a complex environment, attempting to navigate to the exit of the maze during a series of trials at training and again at delayed retest. **(A)** Screenshot of the participants' view, including a landmark (sphere). **(B)** Overhead view of a portion of the maze (not viewable by participants).

tant from the exit, with the order of starting positions counterbalanced across participants. These task features encourage the use of spatial strategies requiring the formation of hippocampus-dependent cognitive maps. Trials ended when participants reached the exit of the maze, or after a maximum of 10 min. Retesting consisted of three additional trials following the same starting point order as during training, but without the 5-min exploration period.

Performance Measures and Data Analysis

As in our previous research,[21] we first calculated completion time (sec) for each trial. However, because improvement in completion time is a measure that may reflect both increased knowledge of the maze layout and increased speed of movement through the environment, we also separately examined independent measures of navigation accuracy and speed. In order to facilitate analysis of movement behavior during the task, the virtual maze space was divided into a 20 × 20 grid. Accuracy measures included distance traveled to the exit (total number of steps as measured by grid squares) and backtracking (number of unique positions / distance traveled), which measures the extent to which participants did/did not retrace their steps while navigating toward the maze exit. Low backtracking scores are achieved when participants repeatedly perseverate down dead ends or move in circles. Navigation speed (distance traveled/min) measured the number of maze grid squares crossed per

Figure 3—Overnight improvement in navigation accuracy and backtracking. **(A-C)** Relative to wake control participants, participants who slept after learning exhibited significantly more improvement in completion time (sec), distance traveled (number of grid squares traversed to the goal), and backtracking (unique positions/total grid squares traversed). **(D)** Posttraining sleep did not facilitate navigation speed (grid squares/min). Error bars = standard error of the mean.

Figure 4—Detail on maze performance data. Top, Mean completion time by group. Bottom, Mean training and retest scores for distance traveled, completion time, speed, and backtracking. Asterisk indicates significance; P < 0.05. Error bars = standard error of the mean.

unit time. For all measures, overnight improvement was calculated as both raw performance change (mean performance on three retest trials – mean performance on three training trials) and percentage improvement relative to baseline performance (raw performance change/mean performance on training trials). Navigation speed was not correlated with the accuracy measures of distance traveled (r = 0.30, P = 0.11) or backtracking (r = 0.29, P = 0.12).

PSG data were scored offline according to standard Rechtschaffen and Kales criteria.[27] Each 30-sec epoch of sleep was classified as wake, stage 1, stage 2, slow wave sleep (SWS; stages 3 and 4), or rapid eye movement (REM) sleep

Sleep and wake groups are compared using Student *t*-tests. All performance variables were normally distributed, with the exception of percent change in distance traveled, which was moderately negatively skewed (-1.28), and raw change in speed, which was moderately positively skewed (1.83). Homogeneity of variance was verified using the Levene metric. Although homogeneity of variance was not significantly violated (with the exception of the sleep versus wake comparison for retest SSS scores, see below), *t*-tests with unequal sample sizes can amplify the effect of any heterogeneity, and distribution of some variables deviated from normality. To eliminate concerns over these issues, all comparisons were also conducted using the nonparametric Mann-Whitney U test, (see Supplemental Results). These nonparametric analyses confirmed the Results presented in the main text.

RESULTS

During the initial training session, there were no significant differences between wake group participants (trained in the morning) and sleep group participants (trained in the evening) in completion time (P > 0.5), distance traveled (P > 0.1), backtracking (P > 0.1), or navigation speed (P > 0.6), suggesting that time of day did not affect encoding (Figure 4, bottom). When tested 10.5 h later, participants showed significant improvement in completion time (t_{29} = 5.01, P < 0.001), distance traveled (t_{29} = 6.00, P < 0.001), and backtracking (t_{29} = 5.71, P < 0.001). Improvement in these measures of navigation accuracy was accompanied by a significant slowing of navigation speed (t_{29} = 2.40, P = 0.02).

Effects of Sleep on Navigation

As in prior studies,[18,21,23] participants in the sleep group improved significantly more on maze completion time than those who remained awake during the retention interval. Sleep group participants averaged a 34 ± 7% (113 ± 21 sec, mean ± standard error of the mean [SEM]) reduction in completion time, whereas those in the wake group showed only a nonsignificant 6 ± 10% (29 ± 20 sec) reduction (sleep versus wake for raw improvement: t_{28} = 2.38, P = 0.03; % improvement: t_{28} = 2.25, P = 0.03; Figure 3A and Figure 4, top). Additionally, sleep led to a greater reduction in distance traveled than did wake, with sleep group participants traversing 114 ± 16 (39 ± 6%) fewer grid squares at retest, whereas the wake group improved significantly less (traversing 29 ± 24 (6 ± 13%) fewer squares; sleep versus wake for raw improvement: t_{28} = 2.97, P = 0.01; % improvement: t_{28} = 2.68, P = 0.01; Figure 3B and Figure S1). Sleep study participants also improved their backtracking more

than wake study participants ($32 \pm 5\%$ (0.17 ± 0.03) improvement in sleep versus $9 \pm 5\%$ (0.05 ± 0.04) improvement in wake (group differences – raw improvement: $t_{28} = 2.18$, $P = 0.04$; % improvement: $t_{28} = 2.13$, $P < 0.05$; Figure 3C).

In contrast to these measures of navigation accuracy, posttraining sleep did not affect change in navigation speed (grid squares traversed/min) through the virtual environment (wake versus sleep for raw improvement: $P = 0.7$; % improvement: $P = 0.6$; Figure 3D). Rather than increasing, navigation speed actually slowed in both the sleep group (10.9 ± 5.0 squares/min, a slowing of $7 \pm 6\%$) and the wake group (by 7.3 ± 7.6 squares/min, a slowing of $1 \pm 9\%$).

This pattern of results was identical when tests were repeated with nonparametric analysis (Supplemental Results), and was identical when examining the sleep and sleep + awakenings groups separately, with the exception that the effect of sleep on backtracking scores fell short of significance in the sleep without awakenings group ($P = 0.16$). Thus, the effect of sleep was robust. In all cases, sleep led to improvement on measures of maze navigation accuracy, but not on navigation speed through the environment.

Sleep Architecture and Performance

We also examined whether the composition of sleep during the night predicted overnight changes in maze performance in the sleep group. None of the measured sleep parameters correlated with performance. We conducted correlations with both raw time as well as percentage total sleep time spent in each stage of sleep (stage 1, stage 2, SWS, combined NREM (stages 2, 3, and 4), and REM), and found no relationships with raw or percent improvement in any maze performance metric (all P values > 0.25). As with the combined sample, separate analyses of the sleep and sleep + awakenings groups revealed no significant correlations between overnight performance change and either time or percentage of time spent in any sleep stage (all P values > 0.12).

Stanford Sleepiness Scores

Although sleep and wake participants had equivalent SSS scores at training ($P = 0.65$), at retest, sleep group participants reported numerically but nonsignificantly lower SSS scores than wake group participants (2.00 ± 0.21 versus 2.89 ± 0.33 [mean $\pm$ SEM]; t-test for unequal variances: $t_{28} = 1.68$, $P = 0.13$), suggesting that wake group participants could have been less alert at retest than sleep group participants. However, SSS scores at baseline showed no correlation with any measure of VMT performance during training, for either raw or percentage change (all P values > 0.05).

Sex Effects on Maze Performance

At baseline training, men completed the maze in a significantly shorter time than women (218 ± 33 sec versus 313 ± 25 sec, mean $\pm$ SEM; $t_{28} = 2.28$, $P = 0.03$). Men also had higher speeds then women during the initial training sessions (81 ± 30 grids/min versus 54 ± 25 grids/min; $t_{28} = 2.51$, $P = 0.01$). However, there were no baseline sex differences in distance traveled to the goal or amount of backtracking. Importantly, sex did not affect sleep-dependent memory consolidation; when sex was included as a factor in 2 (sleep versus wake) × 2 (male versus female) analyses of variance, there were no main effects of sex on change in any performance measure (either raw or percentage), and there were no significant sex × group interactions.

DISCUSSION

Although a number of studies have demonstrated beneficial effects of sleep for learning tasks with a spatial component,[28-32] few have examined realistic navigation tasks in which humans must learn the layout of an environment and display their spatial knowledge by moving through it. Here, we report that accuracy of spatial navigation in a virtual environment was improved following a full night of sleep, relative to an equivalent period of daytime wakefulness. Following sleep, participants were able to navigate to the maze exit in a shorter amount of time by following a more accurate route to the goal. However, neither the total amount of sleep obtained during the night nor the amount of time in any particular sleep stage predicted performance improvements at morning retest. These observations add to a growing body of literature showing that sleep is beneficial for spatial memory consolidation in humans.[18,19,21,33]

Importantly, sleep was not equally beneficial for all performance metrics. Posttraining sleep enhanced navigation accuracy, but did not affect navigation speed. Thus, sleep-dependent improvements in completion time cannot be accounted for by a generally increased speed of movement through the maze. Instead, the effect of sleep was to enhance participants' spatial knowledge of the maze (as evidenced in the effects of sleep on distance traveled and backtracking). Prior studies from Ferrara et al.,[19,33] as well as from our own laboratory,[21] attempted to minimize procedural learning by having participants complete practice training, during which they had the opportunity to become more comfortable with the use of the keyboard navigation controls. However, this is the first study to conclusively demonstrate a significant effect of sleep on the accuracy of spatial memory, independent of speed, thus providing evidence supporting the hypothesis that sleep enhances the formation of hippocampus-dependent spatial maps.

Perhaps surprisingly, participants in both groups actually showed a significant slowing of navigation speed at retest. A slowing of movement in tandem with increased accuracy of navigation and faster completion times might be attributable to the use of greater caution and deliberation as route knowledge develops, so that participants with greater knowledge of the spatial environment move more carefully through the maze.

Although the basic finding that posttraining sleep enhances navigation performance is in line both with our own previous observations[21,23] and those of Ferrara et al.,[18,19] two prior studies from another group[16,17] found that posttraining sleep deprivation had no effect on performance of a similar virtual navigation task. Methodological differences may explain this apparent discrepancy. Of particular relevance may be that the protocol used in these two studies involved much more intensive practice in the environment prior to sleep (an exploration period of up to 1 hour, as compared to 5 min in our own studies), and that due to the constraints of the fMRI paradigm, test trials were very short and uniform in duration, with the primary dependent measure being distance remaining to the goal when trial time expired. In contrast, in our own navigation task, participants had up to 10 min on each trial to solve a highly complex maze. Thus, the

VMT may be more difficult and complex than the navigation task used by Orban et al.[16] and Rauchs et al.,[17] with the spatial map of the environment being less well formed prior to sleep.

At first glance, the lack of correlation between overnight change in maze performance and sleep parameters seems at odds with previous observations. Indeed, several past studies looking at the effect of sleep on declarative memory have reported correlations between over-sleep change in memory performance and the amount or percentage of time spent in NREM sleep stages.[34-37] However, there are also several studies of declarative memory that have failed to find such a relationship,[2,38] or even found negative associations between NREM sleep and declarative memory.[39] Our own prior studies with the VMT have also found no relationship between navigation performance and sleep architecture during a daytime nap.[21,23] Given the inconsistent nature of such correlational findings, we hypothesize that although neural processes critical to memory consolidation are occurring during NREM sleep (as demonstrated in the rodent reactivation literature, for example), the actual number of min spent in NREM is not the critical factor. In fact, the current study adds to a growing body of evidence that performance benefits seen after a night of sleep can be matched by those observed after very short periods of sleep. The performance benefits seen in the current study following a full night of sleep are similar to those previously seen in our earlier VMT studies after a much shorter nap.[21,23] This is a consistent pattern that has also been reported for declarative memory[2,39] as well as both perceptual[40] and motor procedural tasks.[41] It is possible that microarchitectural features of sleep not measured here (e.g., spindles, slow wave activity) may be more important to consolidation than sleep time *per se*.

Limitations

Influence of Circadian Phase and Homeostatic Sleep Pressure

In the current study, sleep and wake groups were trained and tested at different times of day, at different points in the circadian phase, and under different degrees of homeostatic sleep pressure. However, taken together with our prior studies using the same navigation task, circadian confounds do not present a likely explanation for the observed outcome. In our previous nap study,[21] sleep participants and waking control participants were trained and tested at the same circadian time, ruling out any time-of-day influence on the sleep-dependent improvement. In addition, in the current study, time of initial encoding (10:30am versus 10:30pm) had no effect on baseline measures of maze performance, and participants who encoded in the morning versus evening demonstrated similar within-session learning during training. Ratings of task difficulty and engagement were likewise equivalent between sleep and wake groups, as were subjective ratings of alertness, as measured by the SSS.

Possible Effects of Waking Interference

Wake group participants were exposed to a greater amount of new waking experience during the retention interval than those who slept. Although the current study cannot rule out the possibility that detrimental effects of waking interference are the cause of sleep-wake differences, several past findings argue against this possibility. First, studies using a quiet waking control condition, in which sensory interference was reduced, have shown that consolidation is enhanced by sleep, but not quiet rest.[42,43] Second, studies of daytime napping have demonstrated similar benefits of sleep,[21,23] even though wake and sleep groups differed by less than 90mins in the amount of waking during an approximately 6-h retention interval.

CONCLUSIONS

Models of sleep-dependent memory consolidation are strongly informed by rodent studies of sleep following spatial navigation. Understanding the effect of sleep on spatial navigation memory in humans provides a valuable bridge between the rodent literature, demonstrating memory reactivation during sleep, and the human literature demonstrating beneficial effects of posttraining sleep for memory performance. The current study demonstrates that sleep selectively improves measures of navigation accuracy on a 3D-maze spatial navigation task. This finding supports the hypothesis that sleep consolidates recently formed hippocampus-dependent spatial maps.

DISCLOSURE STATEMENT

This was not an industry supported study. The authors have indicated no financial conflicts of interest.

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SUPPLEMENTAL RESULTS

Nonparametric Analysis

Due to moderate violations of normality for some measures, as well as the use of unequal sample sizes, all analyses were confirmed using nonparametric Mann-Whitney U tests. The results uniformly confirm those reported in the main text. A Mann-Whitney analysis of the effect of sleep versus wake on completion time revealed significantly greater improvement in participants who slept, relative to wake (U = 42.0, P = 0.02; percent completion time U = 38.0, P = 0.01). Sleep also benefited the improvement in distance traveled to the goal (U = 35.0, P < 0.01; percent distance traveled U = 41.0, P = 0.02), as well decreases in backtracking (U = 37.0, P < 0.001; percent backtracking U = 39.0, P = 0.01).

Mann-Whitney analysis of the change in speed again supported our parametric results, showing no difference between the sleep and wake groups (U = 93.0, P = 0.96; percent speed U = 85.0, P = 0.68).

Within-Session Learning at Training

A 2 (sleep versus wake) × 3 (Training Trial 1-3) repeated-measures analysis of variance for completion time found no differences between sleep and wake groups in within-session learning across the training period (P = 0.48). Similar analysis for our other measures revealed identical results with no differences between sleep versus wake across the training session (all P values > 0.05). This indicates that at training both groups had similar learning rates.

Table S1—Sleep architecture and quality

	All sleep participants (n = 21)	Sleep w/o awakenings (n = 11)	Sleep + awakenings (n = 10)
TST (min)	411.2 ± 55.2	437.5 ± 46.8*	382.2 ± 50.7*
Stage 1 min	23.2 ± 11.2	21.2 ± 10.8*	25.4 ± 11.9*
Stage 2 min	241.3 ± 48.0	262.7 ± 43.2*	217.7 ± 43.3*
SWS min	76.9 ± 27.3	73.0 ± 21.9	81.3 ± 32.8
REM min	69.8 ± 25.0	80.6 ± 26.0*	57.9 ± 18.5*
Stage 1 %	5.9 ± 3.1%	5.0% ± 2.7%	6.8% ± 3.2%
Stage 2 %	58.5% ± 7.4%	60.1% ± 7.6%	56.7% ± 7.0%
SWS %	18.9% ± 6.6%	16.7% ± 4.5%	21.4% ± 7.9%
REM %	16.8% ± 5.1%	18.3% ± 5.6%	15.1% ± 4.3%
% Sleep efficiency	85.7% ± 11.5%	91.2% ± 9.7%*	79.6% ± 10.6%*

Data are shown both for all sleep participants combined, and separately for those who were and were not awakened for mentation reports (see Methods). Means ± standard deviation; TST, total sleep time; %, stage as % of TST; SWS, slow wave sleep (stages 3 and 4); *P < 0.05.

Table S2—Effect of sleep in groups with and without awakenings

	Wake vs Sleep w/o Awakenings		Wake vs Sleep + Awakenings	
	t	P	t	P
Completion time	2.11	0.05	2.33	0.03
Distance traveled	2.05	0.05	3.29	0.04
Backtracking	1.45	0.16	2.27	0.04
Navigation speed	0.32	0.75	0.38	0.70

Both sleep groups showed greater performance improvement in completion time, distance traveled, and backtracking, relative to the wake control group. t- and P values derived from independent-samples t-tests on raw change in performance measures.
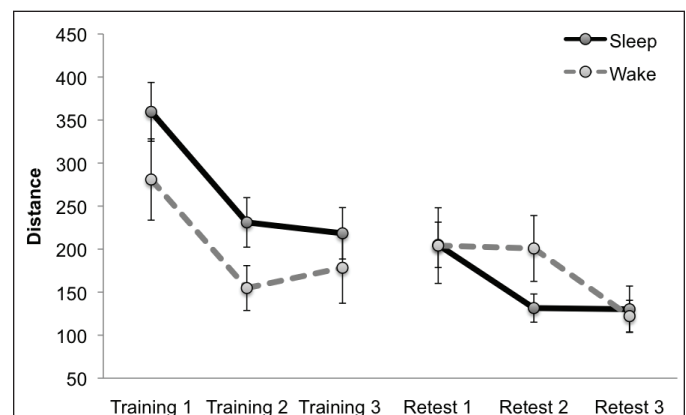

Figure S1—Distance traveled across training and retest trials, in sleep and wake groups. Error bars = standard error of the mean.