

Dreaming of a Learning Task Is Associated with Enhanced Sleep-Dependent Memory Consolidation

Erin J. Wamsley,¹ Matthew Tucker,¹ Jessica D. Payne,^{1,2,3} Joseph A. Benavides,¹ and Robert Stickgold^{1,*}

¹Beth Israel Deaconess Medical Center and Harvard Medical School, Department of Psychiatry, Boston, MA 02215, USA

²Department of Psychology, Harvard University, Cambridge, MA 02138, USA

Summary

It is now well established that postlearning sleep is beneficial for human memory performance [1–5]. Meanwhile, human and animal studies have demonstrated that learning-related neural activity is re-expressed during posttraining nonrapid eye movement (NREM) sleep [6–9]. NREM sleep processes appear to be particularly beneficial for hippocampus-dependent forms of memory [1–3, 10]. These observations suggest that learning triggers the reactivation and reorganization of memory traces during sleep, a systems-level process that in turn enhances behavioral performance. Here, we hypothesized that dreaming about a learning experience during NREM sleep would be associated with improved performance on a hippocampus-dependent spatial memory task. Subjects were trained on a virtual navigation task and then retested on the same task 5 hr after initial training. Improved performance at retest was strongly associated with task-related dream imagery during an intervening afternoon nap. Task-related thoughts during wakefulness, in contrast, did not predict improved performance. These observations suggest that sleep-dependent memory consolidation in humans is facilitated by the offline reactivation of recently formed memories, and furthermore that dream experiences reflect this memory processing. That similar effects were not observed during wakefulness suggests that these mnemonic processes are specific to the sleep state.

Results and Discussion

Subjects were trained on a virtual navigation task and then retested on the same task 5 hr after initial training (see [Experimental Procedures](#) and [Figure 1](#)). As previously observed with the same task [11], subjects who napped following training improved significantly more at retest than those who remained awake during the retention interval (wake improvement = 25.6 ± 56.9 s [mean \pm standard error of the mean], $n = 49$; sleep improvement = 187.9 ± 41.8 s, $n = 50$; main effect of condition: $F_{1,95} = 5.34$, $p = 0.02$; see [Experimental Procedures](#) for analysis details).

Dreaming of the Task Predicts Improved Performance at Retest

Task-related mentation was strongly associated with enhanced performance at retest, whether measured by

questionnaire or by open-ended verbal report (see [Experimental Procedures](#)). In the forced-choice questionnaire protocol (see below), participants in the sleep group who reported maze-related mentation following task training ($n = 12$; 55%) improved significantly more at retest than sleep participants without maze-related mentation ($n = 10$, $t_{20} = 4.02$, $p < 0.001$; see left two columns in [Figure S1](#) available online). In contrast, although a number of wake participants also reported maze-related mentation on the questionnaire ($n = 11$; 40%), this waking mentation was not associated with improved performance ($p > 0.8$; [Figure S1](#), right two columns). Thus, as hypothesized, task-related mentation was associated with enhanced performance only when it occurred in subjects who slept, and not in those who remained awake (2 [condition: wake/sleep] \times 2 [mentation: related/unrelated] analysis of variance [ANOVA]: interaction: $p = 0.006$; main effect of mentation: $p = 0.01$; [Figure S1](#)).

The same pattern was evident when examining open-ended verbal reports ([Figure 2A](#); see also [Figure 3](#)). The four participants in the sleep group (8%) who made reference to the maze in their verbal dream reports ranked among those with the largest postsleep performance improvements in the sample (Mann-Whitney rank-order test: $U = 14.0$, $p = 0.005$; [Figure 2A](#)), improving 10-fold more than sleep participants ($n = 46$) without task-related reports ($t_{48} = 3.88$, $p = 0.0003$; Welch's test for unequal variance: $t_{1,5.96} = 52.8$, $p = 0.0004$; [Figure 2A](#)). Three of these subjects reported task-related mentation at sleep onset (following at least one minute of continuous sleep), whereas the fourth reported a maze-related dream after awakening from stage 2 sleep at the end of the nap period. Again, maze-related verbal reports from subjects in the wake group were not associated with improvement in completion time, with the two wake group subjects who reported thoughts of the maze task performing similarly to the wake group as a whole ([Figure 2A](#); $p > 0.6$ for effect of mentation within wake group; 2 [condition: wake/sleep] \times 2 [mentation: related/unrelated] ANOVA: main effect of mentation: $F_{1,95} = 6.94$, $p = 0.009$; condition \times mentation interaction: $F_{1,95} = 3.11$, $p = 0.08$).

Task-Related Reports Are Not Veridical Reiterations of the Learning Experience

Maze-related elements of the verbal reports are listed in [Table S1](#). Surprisingly, none of these six reports consisted of exact, veridical “replays” of the learning experience. The reports do not, for example, describe the specific objects, locations, or routes of which the task was comprised. Instead, although participants' reports were unquestionably related to the maze, they consisted of remote associations and memories thematically related to the task, or of isolated fragments and thoughts about the maze navigation experience. Two subjects reported hearing the music associated with the task, one subject reported thinking of the upcoming retest, and three reports described other “maze-like” environments (see [Table S1](#)). This lack of exact replay mirrors that observed in animal studies of neuronal memory reactivation, in that patterns of neural activity in rodent sleep statistically resemble patterns seen in the same networks during prior waking

*Correspondence: rstickgold@hms.harvard.edu

³Present address: Department of Psychology, University of Notre Dame, Notre Dame, IN 46556, USA

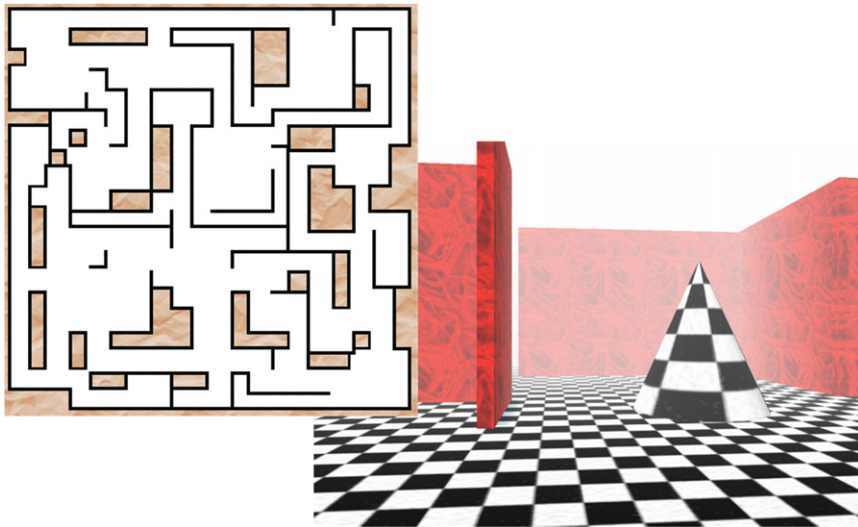


Figure 1. Virtual Maze Task

In this spatial memory task, subjects first learned the layout of a complex maze (left, level 3 is shown). Route memory was then probed across a series of trials as subjects repeatedly navigated to a specified goal point, beginning from pseudorandomized starting locations. An example view of the maze environment is pictured at right. For summary of task-related mentation, see Table S1.

experience but are never strictly identical to those activity patterns [6–8]. Similarly, subjective reports in the present study suggest that memory consolidation in sleep is not necessarily associated with the veridical reiteration of an experience, at least within conscious awareness.

Baseline Performance Predicts Task-Related Dreaming

Although subjects reporting task-related mentation on the questionnaire measure performed similarly at baseline

to those who did not ($p > 0.6$), those with maze-related verbal reports were among those who performed most poorly at training, completing the maze significantly more slowly at baseline than other subjects ($t_{97} = 2.14$, $p = 0.03$; Figure 2B). Critically, however, these subjects with maze-related verbal reports continued to show enhanced improvement even when baseline performance was included as a covariate ($F_{1,47} = 9.00$, $p = 0.004$; Figure 2B), indicating that poor performance at baseline alone cannot explain the memory enhancement associated with task-related dreaming. In summary, it appears that those subjects who reported dreaming about the task also experienced greater difficulty in learning the maze and, having continued to process this information during subsequent sleep, improved more than other subjects at retest.

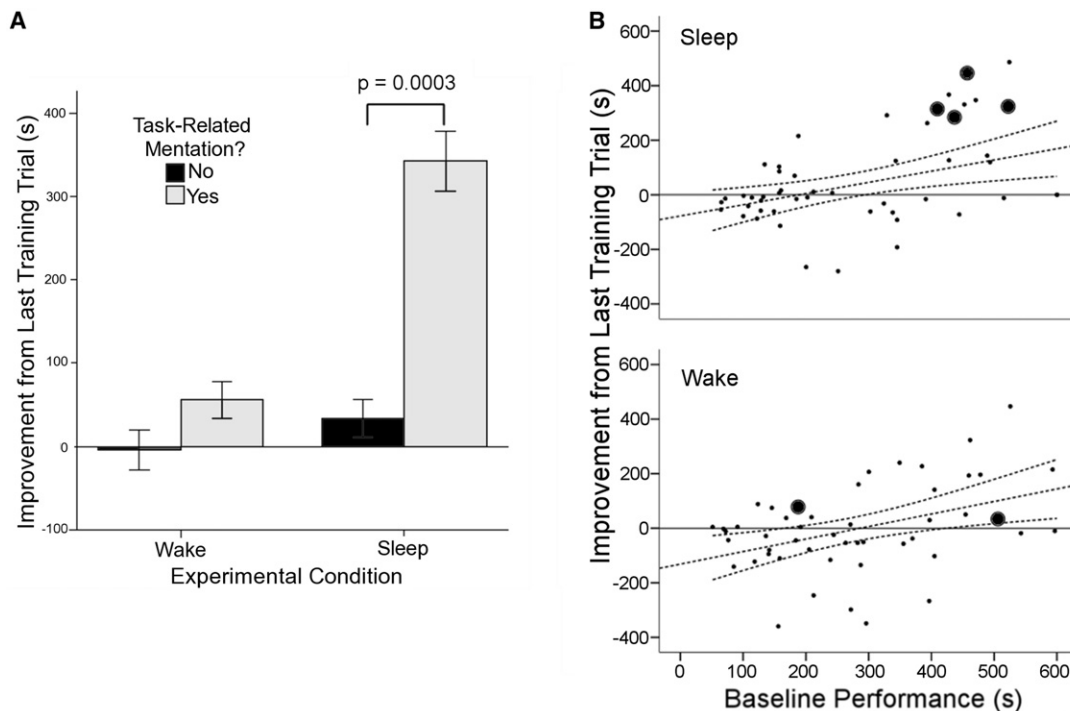


Figure 2. Participants with Maze-Related Verbal Reports Improved More Than Other Subjects at Retest

(A) Sleep subjects with verbal reports related to the maze improved 10-fold more at retest than did participants without task-related mentation. In contrast, thoughts about the task while awake did not provide a similar benefit. Error bars indicate standard error of the mean.

(B) Baseline performance was a strong predictor of later improvement (regression lines and 95% confidence interval lines for all subjects). Sleep participants reporting maze-related dreams ($n = 4$, large circles) were among those with the poorest baseline performance but improved significantly more at retest than other poor performers. In contrast, subjects who reported thoughts of the maze task while awake ($n = 2$, large circles) did not differ from others in terms of baseline performance and improved similarly to those with comparable baseline performance. See also Figure S1.

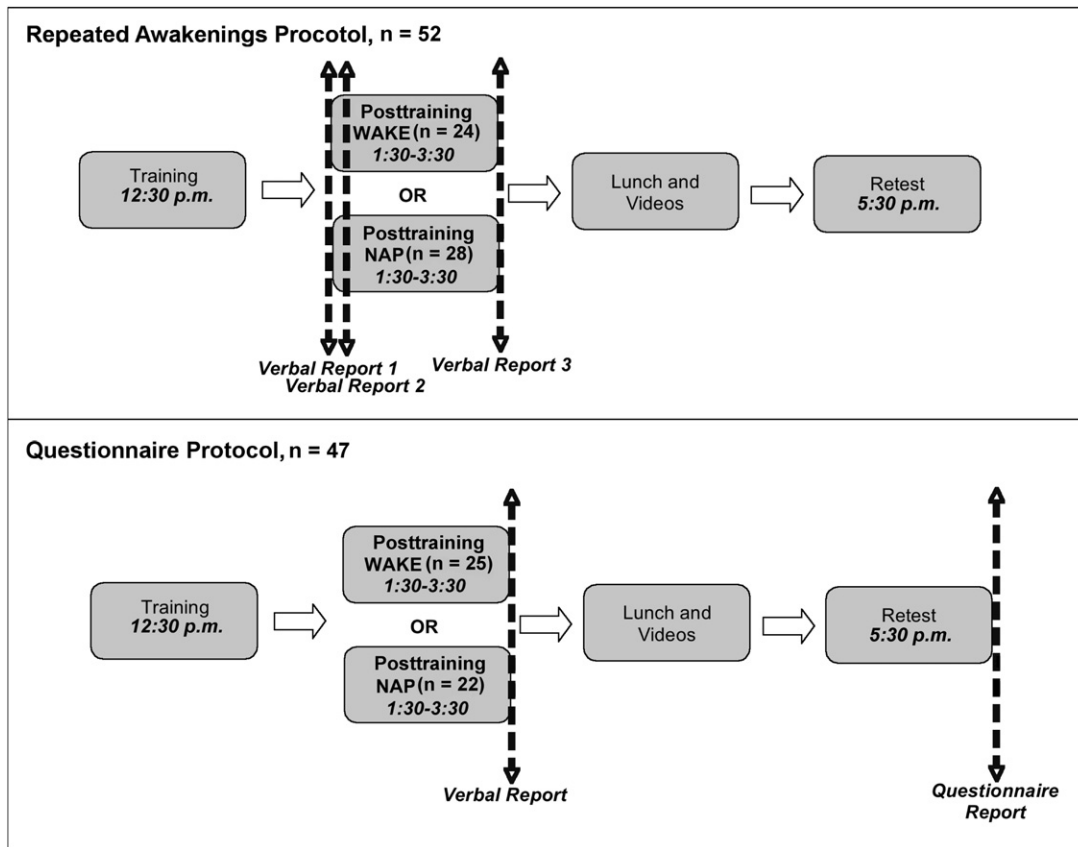


Figure 3. Protocol for Collection of Subjective Reports

“Repeated awakenings protocol” participants ($n = 52$) were interrupted for reporting during the sleep onset period and provided a total of three verbal reports during the posttraining sleep/wake period. “Questionnaire protocol” participants ($n = 47$) were not interrupted during sleep onset and instead provided only one verbal report at the end of the nap, in addition to completing a questionnaire regarding task-related mentation at the end of the study. Total sleep time did not differ between these participant subsets ($p > 0.3$).

Sleep Architecture and Performance

Subjects obtained an average of $45.0 (\pm 16.2$ standard deviation) minutes of nonrapid eye movement (NREM) sleep during the postlearning nap (see Table S2). However, amount of sleep obtained was not correlated with improvements in performance at retest, nor did amount or percent of time in any individual sleep stage predict performance. In light of previous studies using hippocampus-dependent tasks, however, this lack of correlation between performance and sleep architecture is not particularly surprising. Total sleep time does not appear to be an important predictor of sleep-dependent consolidation for hippocampus-dependent memory, with even brief periods of sleep leading to performance benefits similar to those following a full night of sleep [1, 12, 13]. Meanwhile, although a substantial body of literature suggests a causal connection between NREM sleep and hippocampus-dependent memory [1–3, 9, 10, 14–19], reports of significant correlations between amounts of NREM sleep and performance have been the exception rather than the rule. It may be that “sleep stage” categorization is unable to capture the more specific electrophysiological and neurochemical features on which neural plasticity in the sleeping brain depends.

Memory Reactivation and Cognition in NREM Sleep

These cognitive data link postsleep performance improvements to the reactivation of specific task-related memories

in the sleeping brain, as displayed in dream content. As such, the present data argue against nonspecific accounts of the mnemonic benefits of sleep, such as the “interference hypothesis” holding that sleep is beneficial primarily because of an absence of sensory input that might otherwise interfere with task memory (e.g., [20]), or the synaptic homeostasis model, which suggests that all synapses are equivalently activated and modified during sleep [21]. To the contrary, an association of postsleep performance with specific task-related mnemonic content suggests that the performance benefit of sleep is indeed a result of the reactivation of specific memories in the sleeping brain.

Contrary to popular notions of dreaming, reports of mental activity are quite common in NREM sleep [22, 23]. Here, we focused on NREM because of its apparent close relationship to hippocampus-dependent memory consolidation in humans [1–3, 24] and its association with robust memory trace reactivation in rodents [6, 7, 25]. That three of four sleep group verbal reports mentioning the maze were collected from very early in the sleep period (following as little as one minute of sleep) is not surprising, because the animal literature indicates that memory reactivation during NREM is strongest immediately following learning [7, 8, 26]. Human studies also suggest that effects of learning on sleep electroencephalography (EEG) are most visible shortly after sleep onset (e.g., [27, 28]), and our own previous work has detected effects of learning on

sleep onset mentation, but not on dreams recalled the following morning [29, 30].

Critically important is the finding that memory enhancement in the present study was selectively predicted by related mentation during sleep, whereas thinking of the maze during wakefulness was unrelated to later performance. That this waking “rehearsal” of the maze did not benefit subsequent performance indicates that these mnemonic processes active in sleep are in fact specific to the sleep state and suggests that general levels of motivation and engagement cannot easily account for the observed results; more motivated subjects do not simply think about the task more and try harder to improve their performance at retest. Furthermore, this observation points to the importance of the neurophysiological state within which memory reprocessing occurs. NREM sleep is characterized by dramatic neurochemical and electrophysiological changes thought to facilitate memory consolidation [2, 9, 24, 31–34], including a sharp drop in acetylcholine levels [34, 35] and the emergence of 12–15 Hz sleep spindles in the cortical EEG that are temporally correlated with high-frequency EEG “ripples” in the hippocampus [15, 36–38].

As a final note, it is important to distinguish this sleep-dependent improvement from the mental rehearsal during waking that has previously been shown to improve spatial performance [39, 40]. These rehearsal effects are typically seen after repeated, intentional mental reiterations of learned material. In contrast, our data reflect improvement correlated with naturally occurring thought and imagery related to, but distinctly different from, the learned material and do not reflect intentional “rehearsal” of learned information. Future research might fruitfully compare the effects of intentional rehearsal during wakefulness to spontaneous task-related mentation during sleep.

Conclusions

We observed that dreaming of a spatial learning task predicted enhanced postnap memory performance. However, it is not our contention that dream experiences cause memory consolidation during sleep. Instead, we propose that task-related dream experience and the subsequent behavioral enhancement of memory performance both result from an underlying process of memory reactivation and consolidation in sleep. Thus, dreaming may be a reflection of the brain processes supporting sleep-dependent memory processing. In combination with prior brain imaging and cellular-level analyses, our data also provide evidence at the phenomenological level that sleep-dependent memory processing is not necessarily associated with offline reiteration of recent experiences in their original form. Instead, memories may be enhanced in part through a more nuanced process that slowly integrates critical elements of recent experience into established remote and semantic memory networks, facilitating the gradual evolution of more flexible, and ultimately more useful, memory representations.

Experimental Procedures

Participants

Participants ($n = 99$) included 55 female and 44 male college students, ages 18–30. By self-report, all subjects were free of psychiatric and sleep disorders and of medications known to interfere with sleep. Subjects were instructed to abstain from alcohol, caffeine, and other drug use in the 24 hr prior to the study and to maintain a regular sleep schedule prior to participation, and they filled out a three-day sleep log documenting their prestudy sleep schedule. The protocol was approved by the institutional review board of Beth Israel Deaconess Medical Center.

Procedures

Subjects were trained on a virtual navigation task at 12:30 p.m. and were retested at 5:30 p.m., 5 hr after initial training. Participants arrived at the laboratory at 11:00 a.m., where they gave written consent and were wired for polysomnographic (PSG) recording. Wake subjects were also wired for PSG but were not recorded. At 12:30 p.m., participants filled out the Stanford Sleepiness Scale (SSS) [41] and began training on the maze task (see below). Training lasted approximately 45 min. Following training, subjects were informed of group (wake or sleep) assignment. During the subsequent retention interval, sleep participants ($n = 50$) lay down for a 90 min sleep opportunity, while wake subjects ($n = 49$) remained awake in the laboratory. Wake subjects began the retention interval with a 20 min period of “quiet wakefulness,” during which they sat silently, not engaged in any particular activity, after which they were allowed to watch videos until retesting. Sleep subjects slept in a darkened room while EEG, electrooculography (EOG), and electromyography (EMG) were monitored and recorded. Because of our theoretical focus on NREM processes, restricting subjects’ sleep to NREM stages was critical to the present design, allowing analysis of the effects of NREM sleep in the absence of the confounding influence of REM. Thus, participants were awoken at the first signs of REM. This procedure follows from prior work addressing the effects of NREM sleep on memory [1, 42] and allows the isolation of NREM-specific physiology. See Table S2 for sleep architecture data.

Collection of Mentation Reports

Prior to the posttraining sleep or wake period, subjects were instructed that when prompted, they should provide a detailed verbal report of “everything that was going through your mind.” During the sleep onset period, dream recall is exceptionally high [43–46], and experimental awakenings can yield dream reports related to presleep learning as much as 45% of the time [29]. However, in the present study there was a concern that interruptions at sleep onset would disrupt the nap, reduce total sleep time (TST), and interfere with memory consolidation. Thus, two complementary methods were used to assess whether task-related thought and imagery were present (see Figure 3). One group of subjects (“repeated awakenings protocol,” $n = 52$) was prompted to provide three open-ended verbal reports of their current subjective experience during the posttraining period. For sleep subjects, these reports were elicited (1) just prior to the initiation of sleep, (2) after one minute of continuous sleep (“sleep onset” reports), and (3) at the termination of the nap period. As a control for any sleep disruption introduced by awakening subjects during the initial minutes of the nap, a second group of subjects (“questionnaire protocol,” $n = 47$) was not interrupted for reports during sleep onset, providing only one open-ended verbal report at the termination of the sleep period. The two awakening protocol groups did not differ significantly in TST, indicating that sleep onset interruptions in the repeated awakenings protocol did not overtly interfere with their ability to sleep ($t_{48} = 0.87$, $p > 0.3$). Thus, our primary analyses treated these subsets as a single subject group. Participants in the questionnaire protocol further answered a forced-choice question at the end of the study, reporting whether they had experienced any task-related mentation during the period between training and retesting (see Figure 3). Specifically, they were asked, “During the time in between when you first saw the maze and when you were tested on it again, were you thinking about, dreaming about, or imagining the maze game? (Yes/No).”

Verbal reports were classified as related to the maze-learning task only in cases where the maze task was explicitly and unambiguously mentioned in the report (see Table S1). Overall, whereas 100% of wake subjects queried were able to provide at least one mentation report, 22% of sleep subjects were unable to recall any mental experience in response to the prompt (or prompts) delivered.

Following a 30 min lunch break, all subjects watched PG-rated videos in the laboratory until retest (Figure 3). Study staff monitored participants in order to ensure that napping did not occur. At 5:30 p.m., subjects again filled out the SSS and were then retested on the maze task. No between-group differences were observed in SSS scores, gender distribution, age, trait dream recall frequencies, or prestudy sleep schedule (Table 1).

Virtual Maze-Learning Task

The task was a simple 3D graphical environment designed with Abashera maze editor software (Max Magnus Norman Software; http://maxmagnusnorman.com/abashera_free_3d_game.shtml) (Figure 1) and implemented on a PC computer. The maze did not include unique landmarks, and participants began each trial from a different starting point, thus encouraging the use of a hippocampus-dependent spatial strategy

Table 1. Participant Characteristics

	n	Baseline Performance (Last Training Trial)	SSS at Training	SSS at Retest	Age	% Female	Trait Dream Recall	Mean Bed Time from Prestudy Log	Mean Wake Time from Prestudy Log
Wake group	49								
Related mentation	2	231.5 ± 207.7 s	2.0 ± 0.0	2.5 ± 0.7	20.5 ± 2.12	100%	3.00 ± 0.00	12:48 ± 1:50	8:45 ± 0:21
No related mentation	47	255.2 ± 122.3 s	2.9 ± 1.0	2.8 ± 1.0	20.9 ± 2.40	50%	2.90 ± 0.53	12:20 ± 1:08	8:24 ± 0:46
Sleep group	50								
Related mentation	4	538.5 ± 123.0 s	2.8 ± 1.3	2.3 ± 0.5	21.0 ± 1.41	50%	3.00 ± 0.00	12:03 ± 0:31	8:17 ± 0:40
No related mentation	46	255.1 ± 201.2 s	2.8 ± 1.0	2.0 ± 0.8	21.5 ± 2.98	50%	2.86 ± 0.69	12:33 ± 1:09	8:35 ± 1:02

SSS indicates Stanford Sleepiness Scale; bed and wake times listed are a.m. Data are presented as means ± standard deviation. There were no significant differences between groups in sleepiness ratings, age, gender distribution, trait dream recall, or sleep schedule prior to the study. Longer completion times indicate poorer baseline performance. Trait dream recall was assessed as number of dreams recalled per week, as reported in the prestudy sleep log. For nap sleep architecture data, see Table S2.

rather than the memorization of a particular path. The 12:30 p.m. training session lasted for approximately 45 min, and consisted of three distinct phases: a skill-level pretest, an exploration phase, and a series of test trials. The development of the skill-level pretest was based on pilot data indicating substantial interindividual differences in baseline maze navigation skills. During this 20 min pretest, participants were asked to repeatedly navigate to particular goal points within mazes of increasing difficulty. In order to equate subjective maze difficulty across participants, subjects were assigned to one of four maze “difficulty levels,” which differed in size and complexity, based on their performance during pretest evaluation. Next, during the exploration phase, subjects spent 5 min exploring a novel maze at their assigned difficulty level, during which time they were instructed to view as much of the maze as possible, and to remember it as well as possible. In particular, subjects were instructed to remember the location of a particular object in the maze (a “tree,” from which all exploration began). Following this exploration period, subjects continued to navigate through the maze environment during a series of three test trials, in which they were instructed to reach the goal point (the “tree”) as quickly as possible. Test trials began from three different starting points equidistant from the goal. The order of starting points was counterbalanced across subjects, and all subjects received the same counterbalanced order at training and at retest. In order to avoid feelings of frustration and to cap training time at a maximum of 1 hr, a cutoff time of 10 min was established for each trial. If a participant failed to reach the goal within 10 min, the trial was terminated and the next trial begun. As in several prior studies employing virtual environment learning tasks (e.g., [47–49]), performance on each trial was defined as time required to reach the goal, here with a maximum of 10 min. Improvement across the course of the study was calculated as the change in performance from the last (third) training trial to the mean performance on three retest trials (trials 4–6) performed at 5:30 p.m.

Data Analysis Considerations

All comparisons described here were based on specific pre hoc hypotheses. Primary analyses employed a 2 (sleep/wake) × 2 (related mentation/no related mentation) ANOVA, followed by planned paired comparisons. Importantly, caution had to be used in applying inferential tests of statistical significance to small and unequal samples, because normality and variance of population distribution is difficult to estimate based on small subject groups. Although tests for heterogeneity of variance were nonsignificant, we took a conservative approach and applied multiple methods to confirm the robustness of small-sample effects. In addition to Student’s t test, we applied nonparametric Mann-Whitney rank-order tests to all comparisons involving small subsamples. Critical contrasts were also conducted with Welch’s unequal variance t test, which compares sample distributions in a manner similar to the t test but does not assume homogeneity of variance. As reported above, these analyses uniformly confirmed our primary results, demonstrating the statistical robustness of the observed effects.

Supplemental Information

Supplemental Information includes one figure and two tables and can be found with this article online at doi:10.1016/j.cub.2010.03.027.

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