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

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Summary

It is now well established that post-learning sleep is beneficial for human memory performance [1–5]. Meanwhile, human and animal studies demonstrate that learning-related neural activity is re-expressed during post-training non-rapid eye movement sleep (NREM) [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 (*n*=99) were trained on a virtual navigation task, and then retested on the same task 5 hours 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 seen 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 5hrs after initial training (see Experimental Procedures and Figure 1). As previously seen using 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 sec (S.E.), *n*=49; Sleep improvement=187.9±41.8 sec, *n*=50; main effect of condition: $F_{1,95}$=5.34, p=.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 (Fig 3, bottom), 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<.001; Supplemental Figure S1, left). 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>.8, Supplemental Figure S1 right). 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) × 2 (mentation: related/unrelated) ANOVA: interaction: p=.006; main effect of mentation: p=.01; Supplemental Figure S1).

The same pattern was evident when examining open-ended verbal reports (Figure 2, left; see also Figure 3). The four participants in the sleep group (8.0%) who made reference to the maze in their verbal dream reports ranked among those with the largest post-sleep performance improvements in the sample (Mann-Whitney rank order test: U=14.0, p=.005; Figure 2, Left), improving tenfold more than Sleep participants ($n=46$) without task-related reports ($t_{48}=3.88$, p=.0003; Welch's test for unequal variance: $t_{1,5.96}=52.8$, p=.0004; Figure 2, Left). Three of these subjects reported task-related mentation at sleep onset (following at least one minute of continuous sleep), while 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 2, Left; p>.6 for effect of mentation within Wake group; 2 (condition: Wake/Sleep) × 2 (mentation: related/unrelated) ANOVA: main effect of mentation: $F_{1,95}=6.94$, p=.009; condition × mentation interaction: $F_{1,95}=3.11$, p=.08).

Task-Related Reports are not Veridical Reiterations of the Learning Experience

Maze-related elements of the verbal reports are listed in Supplemental 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 is comprised. Instead, while participants' reports were unquestionably related to the maze, they consisted of remote associates 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 Supplemental 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 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>.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=.03; Figure 2, Right). 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=.004; Figure 2, Right), 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.

Sleep Architecture and Performance

Subjects obtained an average of 45.0 (± 16.2 S.D.) minutes of NREM sleep during the post-learning nap (see Supplemental Table S2). However, amount of sleep obtained was not correlated with improvements in performance at retest, nor did amount or % 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 [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 post-sleep 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 non-specific accounts of the mnemonic benefits of sleep, such as the "interference hypothesis" holding that sleep is beneficial primarily due to 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 post-sleep 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, as 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 the sleep 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, while 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. Further, 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 post-nap 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 drug use in the 24hrs prior to the study, and to maintain a regular sleep schedule prior to participation, and they filled out a 3-day sleep log documenting their pre-study 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 12:30pm and were retested at 5:30pm, 5 hours after initial training. Participants arrived at the laboratory at 11:00am, where they gave written consent and were wired for polysomnographic (PSG) recording. Wake subjects were also wired for PSG, but not recorded. At 12:30pm, participants filled out the Stanford Sleepiness Scale (SSS) [41] and began training on the maze task (see below). Training lasted approximately 45 minutes. 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 20min 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, EOG, and 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 Supplemental Table S2 for sleep architecture data.

Collection of mentation reports—Prior to the post-training 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 pre-sleep 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 post-training period. For Sleep subjects, these reports were elicited a) just prior to the initiation of sleep, b) after 1min of continuous sleep ("sleep onset" reports), and c) 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>.3). Thus, our primary analyses treat 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 Supplemental Table S1). Overall, while 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(s) delivered.

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

Virtual Maze-Learning Task

The task was a simple 3D graphical environment designed using the Abashera Maze Editor (Magnus Norman Software, 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, rather than the memorization of a particular path. The 12:30pm *training session* lasted for approximately 45 minutes, 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 inter-individual differences in baseline maze navigation skills. During this 20-minute 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 4 maze "difficulty levels", which differed in size and complexity, based on their performance during pretest evaluation. Next, during the *exploration phase,* subjects spent 5 minutes 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 1hr, a cutoff time of 10min was established for each trial. If a participant failed to reach the goal within 10min, 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 10min. 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 5:30pm.

Data Analysis Considerations

All comparisons described here were based on specific *pre hoc* hypotheses. Primary analyses employed a 2(Sleep v Wake) $\times$ 2(related mentation v 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, as normality and variance of the population distribution is difficult to estimate based on small subject groups. Although tests for heterogeneity of variance were non-significant, we took a conservative approach and applied multiple methods to confirm the robustness of small-sample effects. In addition to the Student's t-test, we applied nonparametric Mann-Whitney rank order tests to all comparisons involving small subsamples. Critical contrasts were also conducted using Welch's unequal variance t-tests, which compare 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.

Highlights

- Improved spatial memory performance is predicted by task-related dream experience.

- Task-related thoughts during waking are unrelated to memory performance.

- Findings are discussed in light of models of sleep-dependent memory consolidation.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

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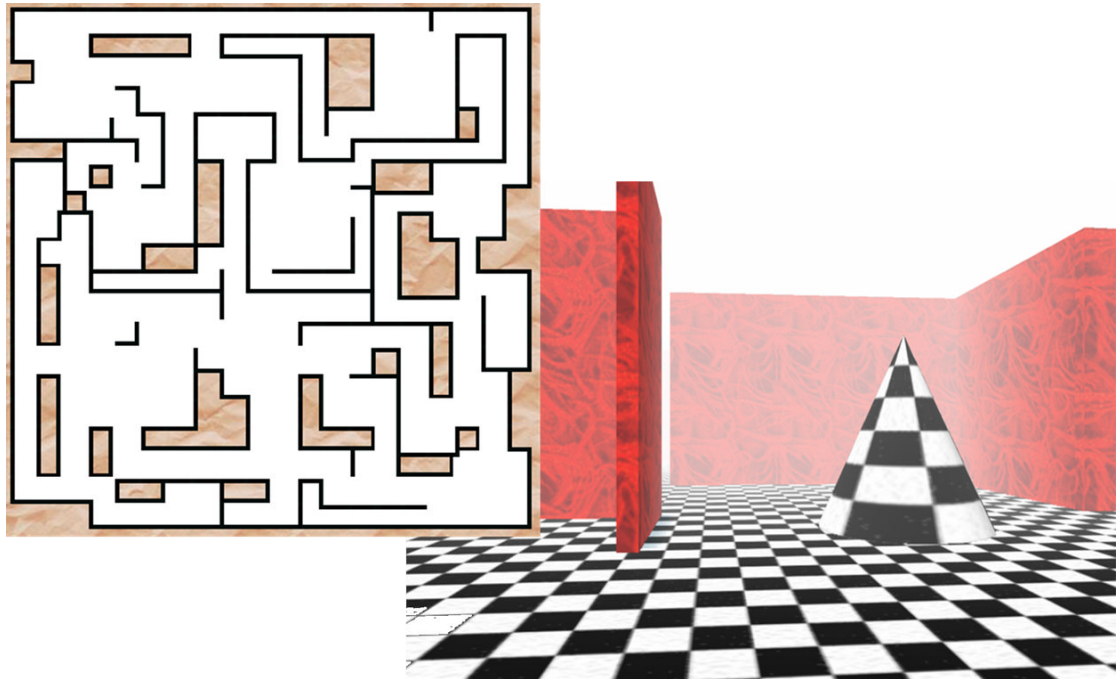
Figure 1. The virtual maze task
In this spatial memory task, subjects first learned the layout of a complex maze (Left, level 3 shown). Route memory was then probed across a series of trials, as subjects repeatedly navigated to a specified goal point, beginning from pseudorandomized starting locations. An example view of the maze environment is pictured (Right). For summary of task-related mentation, see Supplemental Table S1.
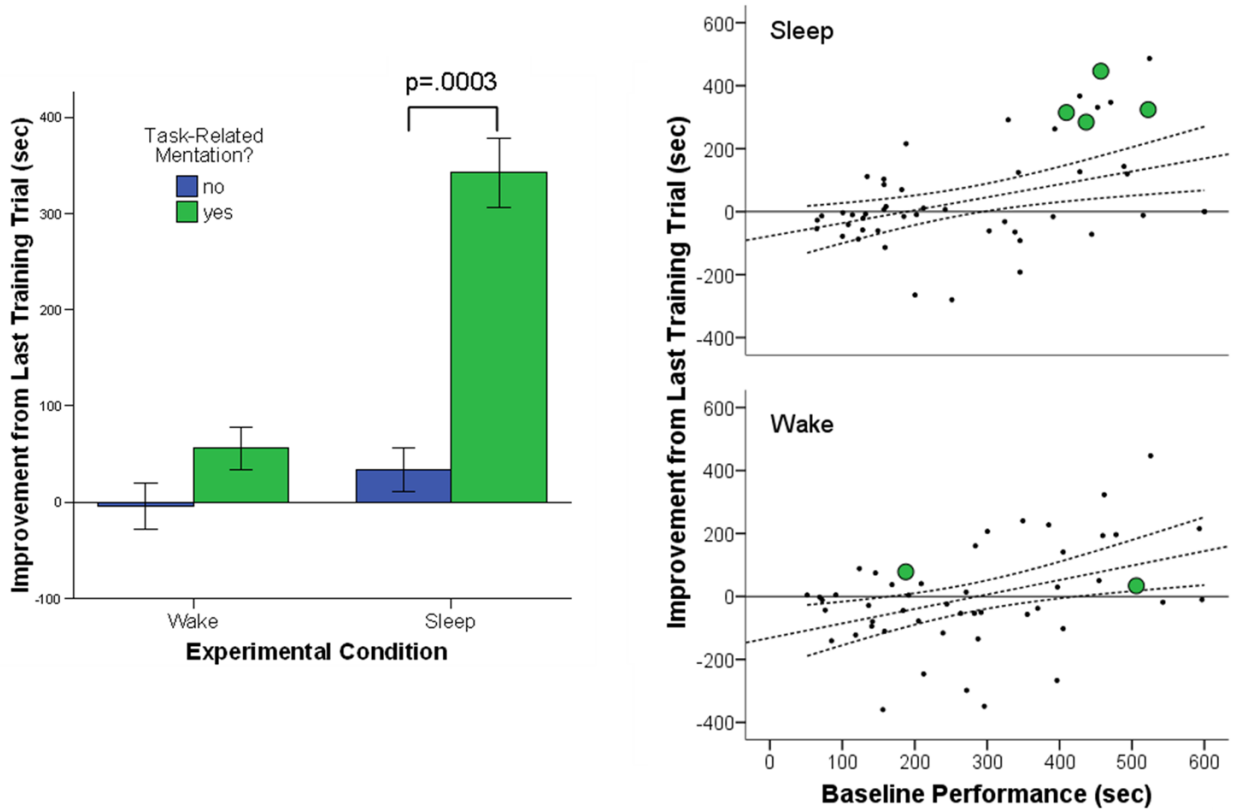
Figure 2. Participants with maze-related verbal reports improved more than other subjects at retest
Left: Sleep subjects with verbal reports related to the maze improved tenfold more at retest than did participants without task-related mentation. In contrast, thoughts about the task during Wake did not provide a similar benefit. Error bars = SEM. Right: Baseline performance was a strong predictor of later improvement *(regression lines and 95% CI lines for all subjects)*. Sleep participants reporting maze-related dreams ($n=4$, large circles) were amongst 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 during Wake ($n=2$, large circles) did not differ from others in terms of baseline performance, and improved similarly to those with comparable baseline performance. See also Supplemental Figure S1.
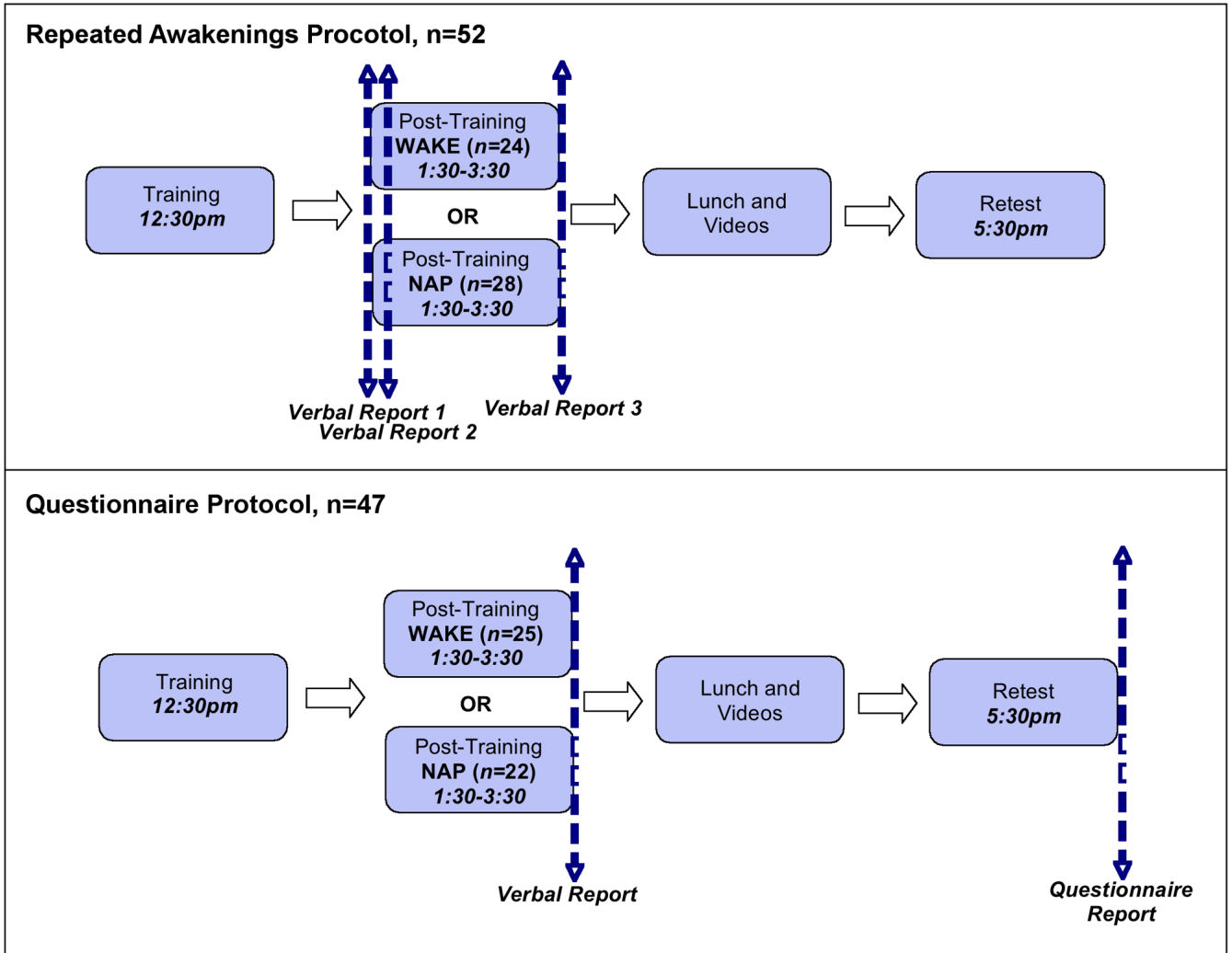
Figure 3. Protocol for collection of subjective reports
"Repeated Awakenings" participants (n=52) were interrupted for reporting during the sleep onset period, and provided a total of three verbal reports during the post-training Sleep/Wake period. "Questionnaire Protocol" participants (n=47) were not 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 (TST) did not differ between these participant subsets (p>.3).

Table 1

Participant Characteristics

	Baseline Performance (Last Training Trial)	SSS at Training	SSS at Retest	Age	% Female	Trait Dream Recall	Mean Bed Time from Pre-Study Log	Mean Wake Time from Pre-Study Log
Wake Group (n=49)								
Related Mention (n=2)	231.5 ±207.7 sec	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 Mention (n=47)	255.2 ±122.3 sec	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 (n=50)								
Related Mention (n=4)	538.5 ±123.0 sec	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 Mention (n=46)	255.1 ±201.2 sec	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

Notes. There were no significant differences between groups in sleepiness ratings, age, gender distribution, trait dream recall, or sleep schedule prior to the study. Means±SD. SSS=Stanford Sleepiness Scale. Longer completion times indicate poorer baseline performance. Trait dream recall is assessed as # of dreams recalled per week, as reported on the pre-study sleep log. For Nap sleep architecture data, see Supplemental Table S2.