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A daytime nap containing solely non-REM sleep enhances declarative but not procedural memory

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Abstract

The specialized role that sleep-specific brain physiology plays in memory processing is being rapidly clarified with a greater understanding of the dynamic, complex, and exquisitely orchestrated brain state that emerges during sleep. Behaviorally, the facilitative role of non-REM (NREM) sleep (primarily slow wave sleep) for declarative but not procedural memory performance in humans has been demonstrated in a number of nocturnal sleep studies. However, subjects in these studies were tested after periods of sleep that contained REM sleep in addition to NREM sleep, and comparison wake groups were subjected to mild sleep deprivation. To add some clarity to the findings of these nocturnal studies, we assessed performance on declarative and procedural memory tasks following a daytime training-retest interval containing either a short nap that included NREM without REM sleep, or wakefulness. Consistent with previous findings we show that, after a comparatively brief sleep episode, subjects that take a nap improve more on a declarative memory task than subjects that stay awake, but that improvement on a procedural memory task is the same regardless of whether subjects take a nap or remain awake. Slow wave sleep was the only sleep parameter to correlate positively with declarative memory improvement. These findings are discussed with reference to the general benefits of napping and within the broader context of a growing literature suggesting a role for NREM-specific physiology for the processing of declarative memory.
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1. Introduction

After more than 40 years of research it has become well known that performance on procedural memory tasks (e.g., visual discrimination, mirror tracing, etc.) is enhanced following periods of sleep containing rapid eye movement (REM) sleep, and that performance on these tasks is impaired following REM sleep deprivation (Fishbein & Gutwein, 1977; Karni, Tanne, Rubenstein, Askenasy, & Sagi, 1994; Mednick, Nakayama, & Stickgold, 2003; Smith, 2001; Stickgold, Whidbee, Schirmer, Patel, & Hobson, 2000). In humans, the evidence is much weaker that REM

sleep promotes processing of declarative (hippocampus dependent) memories (i.e., memories for fact-based information and personal events), which has led some to abandon the idea that sleep-specific physiological processes play any role at all in the processing of declarative memories (Siegel, 2001; Vertes, 2004). However, a strong case has recently been made for the involvement of non-REM (NREM) sleep (Stages 2–4), and in particular slow wave sleep (SWS; Stages 3 and 4), in the processing of declarative memories. A small number of behavioral studies have shown that periods of sleep dominated by SWS enhance declarative memory recall but do not affect performance on procedural memory tasks (Plihal & Born, 1997, 1999a). These studies are complemented by compelling neurophysiological hypotheses outlining the potential

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mnemonic mechanisms of SWS-specific declarative (hippo-campus-related) memory processing (Buzsaki, 1989, 1998; Hasselmo, 1999; Sejnowski & Destexhe, 2000). However, despite these promising findings, there are some outstanding issues to be addressed to more firmly establish this relationship, including the use of research designs that isolate the effects of NREM sleep independent of REM sleep, and the development of research designs that avoid sleep deprivation.

Of the handful of behavioral research designs examining the benefits of sleep for memory processing in humans, the early/late sleep paradigm has consistently revealed a dissociation between memory system tested (procedural versus declarative) and stage of sleep (SWS versus REM) (Barrett & Ekstrand, 1972; Plihal & Born, 1997, 1999a; Yaroush, Sullivan, & Ekstrand, 1971). By comparing performance after the first 3–4 h of nocturnal sleep, which is dominated by SWS, with performance after the last 3–4 h of sleep, during which REM sleep predominates, it is possible to evaluate the relative contribution of these two stages of sleep to processing of different types of memory. It should be noted that the amount of Stage 2 sleep is nearly equal in the early and late halves of the night. Using this design, it has been shown that early sleep facilitates recall of declarative information (paired associates learning and spatial memory), and that late sleep benefits performance on procedural memory tasks (mirror tracing) (Plihal & Born, 1997). These studies also demonstrate that subjects that sleep, either early or late in the sleep period, perform better than their counterparts that stay awake during these intervals. This early/late sleep design has been used to assess the relationship between sleep stage and emotional memory (Wagner, Gais, & Born, 2001), sensory memory (Gais, Plihal, Wagner, & Born, 2000), and recognition memory (Drosopoulos, Wagner, & Born, 2005).

While the findings of the above mentioned studies provide encouraging evidence that SWS facilitates declarative memory processing, several unresolved issues remain. Though it is true that the first half of the sleep period contains increased amounts of SWS, it still contains a substantial amount of REM sleep. It is common for a normal sleeper to cycle through two NREM/REM periods during this 3–4 h sleep interval, which leaves open the question whether it is solely NREM sleep, or the combination of NREM and REM sleep that produce the memory benefits following sleep. Based on a number of behavioral findings it has been suggested that SWS and REM sleep play complementary roles in memory processing (Ambrosini & Giuditta, 2001; Ficca, Lombardo, Rossi, & Salzarulo, 2000; Gais et al., 2000; Stickgold et al., 2000). Also, it is important to consider the striking differences between REM sleep and SWS. REM sleep is characterized by a desynchronized, ''saw-toothed'' theta rhythm in the electroencephalogram (EEG), elevated acetylcholine (ACh) levels, suppressed monoaminergic tone, and heightened cognitive activity, while SWS is characterized by high amplitude, synchronous delta EEG, hippocampal sharp waves, and low ACh levels. While the underlying mnemonic mechanisms of the various sleep stages are not well understood, it is possible that REM sleep could modulate, disrupt, or further enhance NREM (especially SWS) processing of the memory trace.

The present study employs a daytime nap design that specifically isolates the effects of NREM sleep by allowing subjects to obtain only NREM without entering REM sleep. This design not only parses out the selective effects of NREM-related processing of different types of memory tasks, but it also allows for an assessment of the effects of a comparatively brief period of sleep (a 1-h daytime nap) on memory processing. Daytime naps have been shown to beneficially impact a number of performance variables (Takahashi, 2003), and it has recently been demonstrated that a daytime nap that contains REM sleep is associated with performance improvements on a visual discrimination task (Mednick et al., 2003). However, to our knowledge, no studies have been conducted that demonstrate the importance of a NREM daytime nap for improved declarative, but not procedural, memory performance.

Given the evidence supporting a role for NREM sleep in the processing of declarative but not procedural memory, we expected that subjects that obtain NREM sleep (Stages 2–4), but not REM sleep, during a daytime nap would improve more on a measure of declarative memory (paired associates) than those remaining awake during a 6-h training/retest interval. We also predicted that NREM sleep stage amounts (especially SWS) would correlate positively with improvement in paired associate recall. The degree of improvement on a procedural memory task (mirror tracing) was expected to be the same for nap and wake subjects.

2. Materials and methods

2.1. Subjects

Subjects were 29 undergraduate students (13 males, 16 females) of diverse ethnic backgrounds from the City College of New York (ages 18–48, mean = 23). All subjects reported being in good health and were not taking medications that might alter sleep architecture or ability to fall asleep. The 29 subjects (12 nap subjects (6 males, 6 females; ages 18–34, mean = 20.1) and 17 wake subjects (7 males, 10 females; ages 18–48, mean = 25.2)) used for data analysis were selected from a larger initial sample of 33 subjects that completed the experiment. The 12 nap subjects obtained SWS but not REM sleep during the nap. Two subjects from the wake group were excluded from analysis because of exceedingly low baseline scores on the paired associate task (>2 SD from the group mean). One subject did not complete the digit span task, and another did not correctly perform the mirror tracing task, and were therefore excluded from these particular analyses.

2.2. Design and general procedure

Three days before the study subjects signed a consent form, were asked to complete a demographic questionnaire, and also asked to complete a sleep log that recorded bedtime, wake time, and total sleep time prior to the day of the study. They were required to refrain from alcoholic and caffeinated drinks the night before and morning of the study. Subjects were also instructed to eat prior to arriving at the laboratory or to bring food with them to eat in the laboratory. Kitchen facilities in the laboratory were made available to subjects throughout the study. The day of the study,

subjects arrived at 11:30am at the Laboratory of Cognitive Neuroscience and Sleep at The City College of New York. Upon arrival, subjects were familiarized with the sleep chambers and the nature of the study.

To create similar testing conditions prior to baseline learning, sleep and wake subjects had 10 electrodes applied. At approximately 12:15pm subjects underwent the baseline learning phase of the experiment, which took place at two testing areas within the laboratory, one for the mirror tracing task, and one for digit span and paired associates. Digit span was always performed immediately before the paired associates task. These two tasks were counterbalanced with presentation of the mirror tracing task. The initial training phase took approximately 30–40 min to complete.

At 1:00pm the sleep subjects were either taken to a sound attenuated sleep chamber to take a nap (nap group). To address the possibility nap subjects might rehearse the information obtained during baseline learning during the period prior to sleep onset, wake subjects (wake group) were instructed to sit in a chair in another sleep chamber for a period of 10 min to provide them an equivalent period for rehearsal. After this period of 10 min, electrodes were removed from the wake subjects. Wake subjects remained awake in the laboratory until the 6:00pm retest session and were allowed to engage in activities that included looking at magazines or watching pre-selected movies. These passive activities were chosen specifically to minimize the acquisition of new declarative information that could interfere with memory performance at retest.

The sleep group was monitored with digital EEG acquisition software (Gamma System-Grass/Telefactor™) using a five-channel montage (two EEG (C3-A2, C4-A1), two electro-oculography (EOG), and chin electro-myography (EMG)) to monitor sleep during the nap. Sleep stages were scored by a registered polysomnographic technician using the standard criteria (Rechtschaffen & Kales, 1968). The scoring technician was blind to subjects' performance on the memory tasks. Sleep subjects were permitted to attempt to sleep for a period of approximately 1 h. If subjects obtained SWS during this time they were allowed to sleep until it appeared that the first SWS period was coming to an end. After the sleep period electrodes were removed and subjects remained in the laboratory until the retest session. The nap subjects engaged in the same activities as the wake subjects until the retest session. At 6:00pm all subjects were retested on the three tasks in the same order as during the baseline training phase.
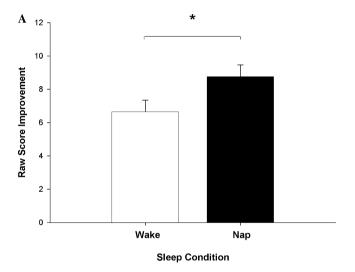
2.3. Memory tasks

2.3.1. Paired associates

Forty-eight semantically related word pairs (e.g., clock-hands) were selected from a larger pool of word pairs used by Plihal and Born (1997). Eight word pairs (four at the beginning and four at the end) were excluded from the response phase to account for primacy/recency effects. Word pairs were presented on a 15″ VGA monitor for 5 s each with a 100 ms interstimulus interval (ISI). Immediately following presentation of the word pair list, subjects were shown in random order the first word of each of the 40 word pairs (minus the four at the beginning and four at the end) and asked to type in the word that completes the pair. After each response was entered the correct answer was displayed for 2 s. At retest subjects were shown the same 40 target words in a different random order, and were asked to type the word that completed the word pair.

In this study, subjects performed just one learning trial, which differs from previous studies that had subjects repeat the response phase until they performed to criterion (usually 60% correct) (Barrett & Ekstrand, 1972; Plihal & Born, 1999a; Yaroush et al., 1971). In those studies, some subjects completed the response phase only once if they reached criterion and others were required to complete the response phase a second time if the number correct was below criterion. Because it is not known whether one versus two or three exposures to the response phase at baseline affects performance at retest, independent of whether subjects sleep or remain awake, we had all subjects complete just one response phase. Our pilot work indicated this to be a more valid testing approach even though it naturally comes at the expense of increased within groups variability on mean number of correctly recalled word pairs at baseline.

Performance was measured as the number of correctly completed word pairs, while improvement was measured as number of word pairs recalled at retest minus number recalled at baseline training. This raw score improvement was also calculated as a percentage improvement over the original baseline score.

2.3.2. Mirror tracing

A five-pointed star was created with a 4 mm wide alley and points that extended 65 mm from the center (Fig. 3A). Subjects sat at a table on which the mirror tracing enclosure was anchored. Subjects placed their hands in an opening in the front of the enclosure that prevented them from directly viewing their hands. A mirror, positioned approximately two feet in front of the subject, allowed subjects to fully view their hands as they traced the star. The star was oriented with the 'start' point facing the subject with an arrow indicating the direction of movement around the star. To control for line thickness, all subjects used a 0.5 mm ballpoint pen. Subjects were asked to work quickly, but to be as accurate as possible. Three mirror tracing trials were administered at baseline and at retest.
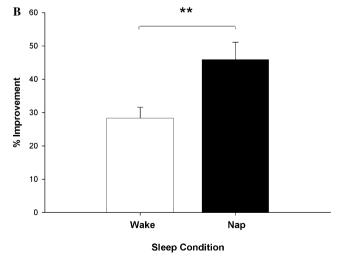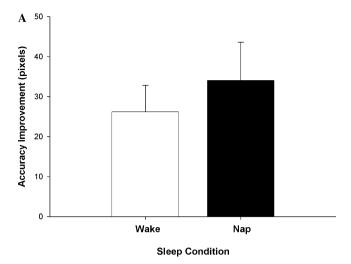

Fig. 1. Improvement in paired associates performance. (A) Improvement is represented as the difference between number of word pairs correctly recalled at baseline training and retest 6 h later. (B) Percentage improvement was calculated as raw number improvement from baseline to retest divided by baseline number correct. Values are presented as means ± SEM. A single asterisk represents a significant between groups difference at $p < .05$; double asterisk, $p < .01$.
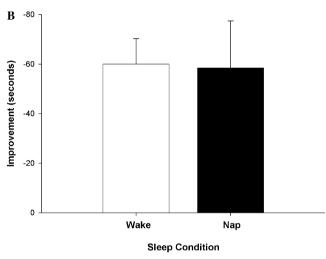
Fig. 2. Improvement in mirror tracing performance. (A) Improvement in accuracy was calculated as average amount (number of pixels) drawn outside the star's boundary at baseline minus retest. Due to a positive skew pixel count was square root transformed. (B) Reduction in time was calculated as average time to complete the star tracings at retest minus average time at baseline. Values are presented as means ± SEM.
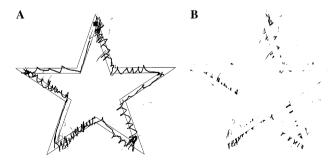

Fig. 3. (A) Example of a mirror tracing trial from one subject. (B) Example of the same mirror tracing star after masking of all marks other than those lying outside the perimeter of the star's boundary.

Performance was measured as average time (in seconds) to complete the tracings, and as a measure of accuracy (amount traced outside the alley of each star measured in pixels). The measurement of mirror tracing accuracy employed represents a novel approach to the issue that bears some

similarity to a technique used in previous research (Plihal & Born, 1997). However, instead of measuring time spent outside of the star's boundary, the number of pixels outside the boundary was calculated. This was done by scanning and saving each traced star image as a .jpg file (Fig. 3A). A mask was created that covered the alley of each star leaving exposed only the tracings that extended beyond the star's boundary (Fig. 3B). The number of black pixels was then counted using a pixel counter and averaged for the three baseline and retest star tracings. Reduction in time was measured as average time to complete the tracings at retest minus baseline, and improvement in accuracy was measured as number of pixels traced outside the star's boundary at baseline minus retest.

2.3.3. Digit span

The digit span test was based on the WAIS-III subtest using only the forward learning part of the test. It was used in this study as a general measure of attention at baseline and to acclimate subjects to the testing environment prior to performing the paired associates task. Numbers were presented serially on a 15″ VGA monitor for 1 s each followed by a 1-s ISI. After the numbers were presented subjects wrote down on a response sheet the numbers in the order they were presented. The first test series consisted of three numbers with each subsequent series increasing by one number until the last series, which contained 10 numbers. After responding to the last series of 10 numbers, subjects then completed a second trial starting again with three numbers and progressing to 10 numbers, but using different number sequences. Digit span always immediately preceded the paired associates task. The same task was administered at retest using different number series. Performance was measured as the number of correctly recalled number series at baseline and retest.

3. Results

A summary of sleep parameters for nap subjects are found in Table 1. The mean total sleep time (TST) was approximately 47 min, roughly one fourth of the total sleep (approximately 190 min) obtained by subjects in the study by Plihal and Born (1997). Of the 47 min approximately 11% was spent in Stage 1, 41% in Stage 2, 21% in Stage 3, and 27% in Stage 4. Therefore, approximately 48% of the sleep period was spent in SWS (Stages 3 and 4), and approximately 90% of the nap was spent in NREM (Stages 2–4). Stage REM does not appear at all. Relevant pre-study sleep variables are presented in Table 2. Analysis of the 3-day sleep log data revealed no differences between the nap and wake groups for number of hours awake prior to the baseline training session ($t_{27} = .50$, $p = .62$), total sleep time the night before the study ($t_{27} = .26$, $p = .80$),

Table 1
Sleep parameters

	Min ± SEM	% of TST ± SEM
SL	11.75 ± 2.50	
TST	47.00 ± 4.13	
WASO	8.92 ± 3.13	
S1	5.17 ± 1.05	11.00 ± 2.30
S2	19.38 ± 1.89	41.23 ± 4.66
S3	9.63 ± 1.85	20.50 ± 3.69
S4	12.80 ± 4.17	27.23 ± 6.66
SWS (S3 + S4)	22.43 ± 4.60	47.73 ± 6.65

Note. SL, latency to sleep onset (first epoch of sleep); TST, total sleep time; WASO, wake after sleep onset; S1–S4, Stages 1–4; and SWS, slow wave sleep.

Table 2
Pre-study variables

	Nap	Wake	t_{27}	p
Wake prior to learning	$4.3 \pm .56$	$4.0 \pm .33$	.50	.62
TST night before study	$7.6 \pm .31$	$7.5 \pm .37$	.26	.80
Mean TST three nights prior to study	$7.3 \pm .42$	$7.2 \pm .35$	.13	.89

Note. Time is measured in h $\pm$ SEM; TST, total sleep time.

or the average total sleep time across the three nights prior to the day of the study ($t_{27} = .13$, $p = .89$).

Subjects in the nap group demonstrated greater improvement at retest than wake subjects, measured as the improvement in number of word pairs recalled at retest ($8.75 \pm .71$ (mean $\pm$ SEM) versus $6.65 \pm .71$; sleep group $\times$ time interaction, $F_{1,27} = 4.16$, $p = .05$; partial $\eta^2 = .133$) and percentage improvement over baseline (45.82 ± 5.22 versus 28.36 ± 3.27; $F_{1,27} = 8.95$, $p = .006$; partial $\eta^2 = .25$) (Fig. 1). Baseline recall of paired associates task for the nap and wake groups did not differ substantially (20.92 ± 1.78 versus 24.12 ± 1.14, $p = .12$). Pearson's product-moment correlations revealed positive, though non-significant, relationships between percentage of SWS in the nap and improvement on the paired associates task (% improvement, $r = .37$, $p = .12$; raw score improvement, $r = .30$, $p = .17$). The inverse was true when percentage improvement on the paired associates task was correlated with percentage of Stage 1 ($r = -.26$, $p = .21$) and Stage 2 sleep ($r = -.40$, $p = .10$). Because of the difference in direction of the correlations for SWS and Stages 1 and 2 with performance, the correlation between TST and percentage improvement was negligible ($r = .03$, $p = .46$).

Mirror tracing data revealed no differences between groups at baseline or retest. Nap and wake groups did not differ at baseline on average accuracy (number of pixels drawn outside the star boundary) (87.73 ± 13.23 versus 75.92 ± 14.28, $p = .69$) or average time to complete the three star tracings (119.06 ± 23.67 versus 113.71 ± 12.75, $p = .83$). Due to a significant positive skew in the distribution of our measure of tracing accuracy (amount drawn outside the star's boundary) for both subject groups, the data were square root transformed. There were no differences between groups on the two measures of improvement–improvement in accuracy (35.67 ± 8.89 versus 26.18 ± 6.67; sleep group $\times$ time interaction, $F_{1,26} = .76$, $p = .39$) or decrease in time to complete the star tracings from baseline to retest (-57.92 ± 17.36 versus -59.96 ± 10.33; sleep group $\times$ time interaction, $F_{1,26} = .006$, $p = .94$) (Fig. 2).

There was not a significant difference in baseline digit span performance nap and wake subjects, although mean performance for the wake group was slightly higher ($5.16 \pm .33$ versus $4.35 \pm .31$, $p = .09$). Both groups demonstrated similar improvement from baseline to retest ($.47 \pm .19$ versus $.26 \pm .25$; sleep condition $\times$ time interaction, $F_{1,27} = 1.06$, $p = .67$). Because digit span is a measure of immediate memory and known not to rely on the hippo-

campus for processing, performance was expected to be uncorrelated with performance on the paired associates. Pearson's product-moment correlations revealed that baseline digit span scores ($r = -.109$) and digit span improvement ($r = -.042$) were not correlated with improvement on the paired associates task.

4. Discussion

Using a research design that specifically isolates the effects of NREM sleep we show that improvement on a paired associates declarative memory task is greater for subjects that take an early afternoon nap than for subjects that remain awake during the baseline-retest interval. This difference in improvement is not observed for the procedural memory task, which lends further support to a growing body of evidence that NREM sleep plays a special role in the processing of declarative, but not procedural, memories. Recognizing that our findings are confined to a specific time period during the day, the results represent the first evidence that a brief daytime nap can significantly benefit declarative memory performance, the practical application of which should be appreciated. Traditionally, time devoted to daytime napping has been considered to be counterproductive in environments requiring mental acuity and substantial memory capacity. Clearly, this assumption may not be warranted given the performance benefits (Takahashi, 2003), procedural memory enhancement (Mednick et al., 2003), and now declarative memory improvement following a daytime nap.

In addition to the practical ramifications of the current findings it is noteworthy that the statistical values representing the effect of NREM sleep on improvement in number of word pairs recalled and percentage improvement over baseline ($F_{1,27} = 4.16$ and $F_{1,27} = 8.95$) are similar in magnitude to the findings of Plihal and Born (1997) ($F_{1,18} = 4.79$ and $F_{1,18} = 4.46$) after a relatively brief period of sleep (47 min), compared to approximately 190 min in the study by Plihal and Born (1997). This similarity could be interpreted to mean that longer periods of sleep recorded in nocturnal studies are not required for early processing of declarative memory. However, it is also possible that other factors, such as circadian influences, could also play a part in this enhanced processing. For example, cortisol levels, which are at their circadian nadir early in the nocturnal sleep period, have been shown to modulate recall of declarative information. In one study, infusion of cortisol during an early period of sleep, which elevated plasma cortisol to levels comparable to morning peak circadian levels, impaired recall of paired associates compared to subjects that received a placebo (Plihal & Born, 1999b). Sleep in the present study was recorded during a time when cortisol levels are at about their circadian midpoint (Weitzman, Schaumburg, & Fishbein, 1966), which may or may not have mediated the effect of sleep in the present study.

While there may exist subtle differences between diurnal and nocturnal sleep, it should be noted that the design for

the present study was based on what is currently known about the general characteristics of NREM sleep-related physiology and its potential to facilitate declarative memory processing. Specifically, the role of NREM sleep for declarative memory processing is strongly tied to the necessary function of the hippocampus for declarative memory processing (Milner, Corkin, & Teuber, 1968; Squire, 1992; Eichenbaum, 1997). It is well known that elevated hippocampal ACh during wakefulness is important for encoding (Hasselmo & McGaughy, 2004), and that suppression of hippocampal ACh during encoding produces noticeable impairments in later retrieval (Rogers & Kesner, 2003). The inverse is true during SWS when low levels of ACh appear to be necessary for optimal consolidation of the memory trace (Gais & Born, 2004). Remarkably, it has been shown that artificially elevating ACh levels in humans during SWS by the intravenous administration of the ACh agonist physostigmine produces marked impairment in recall of paired associates compared to control subjects receiving a placebo (Gais & Born, 2004).

In addition to sleep dependent fluctuations in ACh, there are unique electrophysiological events that occur during SWS that may be intimately linked to information processing. During SWS, low ACh levels in the hippocampus produce a disinhibition of glutamatergic cell groups that generate periodic high amplitude sharp waves and high frequency ripples ($\sim$200 Hz), which are a hypothesized mechanism for the transfer of declarative information from the hippocampus to neocortical targets (Buzsaki, 1989, 1998). These sharp wave/ripple events have been shown to activate efferent projections to entorhinal cortex (Chrobak & Buzsaki, 1994) during SWS, and recent neurophysiological evidence suggests they are closely related to thalamically generated cortical spindles, which occur during Stage 2 and SWS. In fact, it has been shown in rats that the occurrence of sharp waves/ripples is correlated with spindle activity in the medial prefrontal cortex (Siapas & Wilson, 1998), and somatosensory cortex (Sirota, Csicsvari, Buhl, & Buzsaki, 2003). While the temporal sequencing of these events has yet to be clearly defined, these findings nevertheless point to the potential importance of an interaction between thalamocortical spindles and SWS-associated hippocampal events (sharp waves/ripples) for sleep-dependent declarative memory processing.

While the physiological processes described above suggest a putative mechanism for sleep-dependent declarative memory processing, conclusive experimental evidence of the mnemonic function of individual sleep stages has yet to be documented. However, researchers have recently begun to manipulate cortical electrophysiology during SWS in ways that impact memory processing. In a recent study, it was shown that augmentation of the negative DC potential characteristic of the synchronous, high amplitude cortical electrical activity observed during SWS, by application of transcranial direct current stimulation (tDCS), produced a striking enhancement of declarative (paired associates) memory recall compared to subjects that did not receive tDCS (Marshall, Molle, Hallschmid, & Born, 2004). This finding elegantly demonstrates that sleep-related cortical electrophysiology may directly modulate post-sleep declarative memory performance.

Although, the results of the present study are encouraging, we should bear in mind that they are preliminary and that there are a number of issues that should be addressed in the future to more clearly establish the role of NREM sleep for declarative memory processing. First, to strengthen the argument that sleep physiology does not merely permit memory consolidation but represents an active mechanism for memory formation, a strong correlation between amount of SWS and memory improvement should be established. To date, very few studies have reported correlations between sleep parameters and improvements in memory performance. In the present study, correlations between SWS parameters and declarative memory performance were in the hypothesized direction, but fell short of statistical significance. It remains to be seen whether these non-significant correlations are a reflection of the limited amount of sleep obtained by nap subjects, the small subject sample size, or other influences specific to daytime sleep, such as yet unidentified circadian factors.

A second unresolved issue regards the lasting effects of sleep dependent memory enhancement. The present study used a baseline-retest interval of 6 h, which should have allowed for early consolidation processes to occur. However, retesting subjects after longer time intervals following a nap will inform us of the longer term effects of sleep following information acquisition. Mednick et al. (2003) showed that enhanced procedural memory performance on a visual discrimination task was maintained up to 72 h after a nap. It remains to be seen if this finding translates to declarative types of memory.

Acknowledgments

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