Does the "Sleep Effect" on Memory Depend on Sleep or on Night Time?

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Numerous investigations demonstrated superior verbal memory performance after retention intervals of nocturnal sleep as opposed to diurnal wakefulness. However, it is not clear if the effect is attributable to either sleep or circadian phase. The present study therefore examined verbal recall after retention intervals of nocturnal sleep, diurnal wakefulness, and nocturnal wakefulness (sleep deprivation). Forty university students (range 19-30 years) were randomly assigned to one of the three conditions and were tested for cued recall of a paired-associate list 7 h after original learning. In line with previous findings, subjects in the nocturnal sleep condition expressed superior recall when compared to subjects in the diurnal wakefulness condition. However, contrary to predictions, recall performance between the nocturnal sleep and the nocturnal wakefulness condition did not differ significantly. The results raise some doubt on the generalizability of the beneficial effect of sleep on memory. (Sleep and Hypnosis 2006;8(2):61-70)

Key words: sleep, sleep deprivation, memory, retention, circadian phase

INTRODUCTION

It is a well-established fact that recall of verbal information from long-term memory is superior after retention intervals of nocturnal sleep in comparison to retention intervals of daytime wakefulness (1-9). This finding was subsequently termed "sleep effect" (10). However, due to the confounding of the two factors sleep/wake and circadian phase that is inherent in the experimental design used, the effect cannot

independent variable sleep. This leaves the question whether the beneficial effect on memory is mediated by sleep per se or whether it "may actually be due to circadian variables which simply share the same period of time" (6, p. 372). To disentangle both factors, the sleep and the wake condition have to occupy the same nocturnal period.

be attributed unambiguously to the

Though primarily aimed at isolating the differential effects of slow wave sleep (SWS) and rapid eye movement (REM) sleep, partial evidence for a beneficial effect of sleep per se comes from research investigating the first and second half of a 7 h nocturnal sleep separately. With the exception of Wagner et al. (11) all studies in this area found significantly better retention when subjects slept through the first 3-4 h of the night than

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when they were kept awake during the same nocturnal period (10,12-17). However, from these investigations no conclusion about the role of the naturally occurring entire night sleep cycle can be drawn.

Hockey et al. (18) conducted an experiment with four different 5 h retention intervals. Two groups learnt a list of nouns in the late evening and recalled it in the late night. Two other groups had their learning and recall in the early and late morning respectively. One group of each time of day condition was allowed to sleep while the others underwent sleep deprivation during the retention interval. The results indicated a main effect for time of day but not for sleep, thus favoring circadian factors rather than sleep as the critical variable.

To our knowledge, only two studies attempted to compare a full night of sleep with a corresponding period of total sleep deprivation between learning and recall. Idzikowski (19) had subjects learn a list of nonsense syllables in the morning. After 16 h of subsequent daily activity one group went to sleep for 8 h while the other group underwent total sleep deprivation during the same period of night. Despite 16 h of waking activity that preceded the critical night period, free recall, paced recall, and relearning in the morning significantly better results for the sleep group. Nesca and Koulack (6) on the other hand did not find superior memory for the sleep condition on a verbal recognition task when comparing 8 h nocturnal retention intervals that were either filled completely with sleep or wakefulness.

Another critical issue in the research of sleep and memory that has widely been neglected is the problem of insufficient measures of retrieval from long-term memory. As pointed out by Roediger and Guynn "a single test of memory is an imperfect indicator of knowledge" (20, p. 200). Contrary to the well-known forgetting curves of the pioneering work of Ebbinghaus

(21), which indicate a monotonous decline of memory with the passage of time, numerous studies have demonstrated an increase of recall between consecutive tests (22-26). Although the effect of sleep on memory has been investigated by various methods of retrieval (relearning, free recall, cued recall, recognition), only Barrett and Ekstrand (12) adopted the method of repeated recall tests. When comparing retention after sleep during the first and second half of the night, these authors found significantly better recall after the first half on the first test, but not on the second. These results demonstrate that the analysis of only one single recall test is likely to underestimate the amount of information stored in memory and may thus yield misleading results. A similar reason for possibly inaccurate measures of retention is the failure to control for report bias. While it is common practice in recognition tasks to have one measure for the ability discriminate old and new items and one for a potential response bias (27, 28), standard cued and free recall paradigms usually do not include a separate measure of report bias. Thus, standard recall procedures probably underestimate retention of those subjects that have a conservative threshold and therefore tend to withhold a response unless they are quite sure it is the correct one. Such underestimation can easily be circumvented by forced report techniques, which force or at least encourage subjects to guess a response rather than to give no response at all in case of uncertainty (29,30).

The aim of the present study was to further clarify the possible constraints of the beneficial effect of sleep on memory under conditions of circadian phasing and appropriate measures of memory retrieval. We therefore compared memory performance over three different retention intervals of nocturnal sleep, diurnal waking, and nocturnal waking. To effectively exhaust storage in long-term memory, we adopted successive recall trials and, beginning with

the second trial, asked subjects to guess if they were not sure about the correct response. Based on the existing literature we expected to replicate the classical sleep memory effect, that is better retention after nocturnal sleep than after diurnal wakefulness. The critical question was however, whether sleep would still lead to superior recall with circadian factors held constant, i.e. better retention after nocturnal sleep than after nocturnal wakefulness.

METHOD

Subjects

Forty university students (19 male, 21 female) aged between 19-30 years (M=24.3, SD=2.9) participated in the experiment for financial compensation and were randomly assigned to one of the three experimental groups Sleep/Night (n=12), Wake/Night (n=12), and Wake/Day (n=16). Inclusion criteria were non-smoking, regular sleep schedule (7-8 hours nocturnal sleep, sleep latency below 30 min, no excessive daytime napping), absence of any psychoactive medication and sleep disturbances during the last four weeks, no history of neurological or psychiatric illness. Subjects were obliged to refrain from alcoholic beverages, caffeine, and daytime napping 12 h before conducting the experiment. All participants gave signed consent to take part in the study after the study protocol had been fully explained.

Memory testing

For the sake of comparability with a great deal of previous research, memory was probed by a paired-associate list (PAL) of 16 noun pairs. To keep guessing probability low, the stimulus and response words of all pairs were weak associates. All words contained 5-9 letters and had a moderate imagery rating (z-scores between 0.00 and 0.53) (31). The complete list of words is

presented in the Appendix.

Learning was carried out by the study-test method in four consecutive trials. During study trials a computer program presented all 16 pairs in sequential random order with a presentation rate of 1/1500 ms and an interstimulus interval of 1000 ms. During test trials the stimulus words only were presented in sequential random order and subjects had to type the matching response word on a keyboard. Except for the last test trial, which served as a measure of original learning, all responses were followed by feedback about their correctness (displaying "Correct" or "False" for 1 sec). To prevent active rehearsal, subjects had to perform simple additions of three digit numbers for 2 min before and after the last test trial.

The recall session consisted of four consecutive test trials without feedback. Beginning with the second recall test trial subjects were instructed to guess the correct response if they were unsure about it. Memory testing was completed by a final forced-list recognition test (32) that contained all 16 response words together with 16 matching lures of semantic similarity (see Appendix). The computer program simultaneously presented all response words and lures in random order on the left side of the screen. The subjects' task was then to use the computer mouse to move those 16 words to the panel on the right side that they felt were the response words presented during learning.

Design and procedure

The length of the retention interval was 7 h for all three groups. This period was chosen because recent epidemiological surveys (33-35) and laboratory findings (36) demonstrated that seven hours is the average habitual sleep period of healthy young adults.

To ensure that all subjects were fully awake during test sessions, they had to

perform two computerized psychomotor tracking tasks of 3 min duration each, before learning and recall began (see (37) for a similar attempt using a mirror tracing task). The first task required them to follow random movements of a marker on the screen with the computer mouse as closely as possible. On the second task, subjects saw a vertical bar between two fixed bars on the left. and right side of the screen. Due to unpredictable "forces" simulated by the software, the bar continuously tended to move away from the center location in one or the other direction. The task was to compensate those disturbances by moving the computer mouse in the opposite direction thereby avoiding the middle bar hitting one of the outer bars. Each such hit was signaled by a short beep and was scored as an error. However, since fully awakening was the sole reason to deploy both tracking tasks, no data regarding them will be reported in the Results section.

Sleepiness was measured subsequently during learning and recall sessions by a 60 sec finger-tapping task. This task is quickly and easily accomplished by subjects. Yet, it has shown sensitivity to fatigue as indicated by a decline in tapping rate due to hangover effects of sedative drugs (38-41). Subjects had to strike the Enter key of the numerical keyboard block repetitively for 60 sec as quickly as possible. In order to avoid premature disengagement, they were in fact misinformed that they had to tap for 90 sec. However, the software terminated processing keyboard input already after 60 sec. In addition, subjective sleepiness was assessed by the Stanford Sleepiness Scale (SSS) (42,43).

Subjects in the sleep condition were acclimated to the placement of electrodes and the sleep laboratory by spending one adaptation night. To ensure comparability with the two other conditions, the adaptation night was always scheduled two nights before the test night, so that subjects of all

groups would sleep at home the night right before the experiment. In the experimental night, they reported to the laboratory at 22.00 h for placement of electrodes and began memory testing between 23.15 h and 23.30 h, which took about 30 min. Lights were turned off between 23.45 h and 00.00 h, immediately after original learning was completed. Sleep was monitored all night by polysomnography according to standard criteria (44). Awakening from sleep was between 06.45 h and 07.00 h. The retest session began between 07.00 h and 07.15 h.

Subjects in the Wake/Night condition performed learning and recall at 23.30 h and 07.00 h respectively. During the 7 h retention interval, they stayed awake under the control of always two experimenters. They were free to watch videos, read recreational materials, or talk with the experimenters. Consumption of caffeine or alcoholic beverages was prohibited throughout the entire night. Subjects in the daytime condition began learning at 08.30 h. Following this, they were obliged to refrain from caffeine, alcohol, and napping and were dismissed from the laboratory. They returned for recall at 16.00 h.

To prevent any exchange of learning material, all subjects participated individually. Subjects who failed to recall at least four items of the paired associate list during the last trial of original learning were excluded from further analysis and replaced by others. Likewise, subjects in the sleep group who exhibited a sleep latency above 45 min or a sleep efficiency index below 80% were substituted by others. Three participants in the Sleep/Night and Wake/Night group respectively were replaced because they had failed to meet the learning criterion. Two participants in the Sleep/Night group were replaced due to poor sleep quality.

Data analysis

Sleep recordings were analyzed off-line according to standard criteria (44). Relevant

sleep parameters were sleep onset latency, amounts of sleep stages 1, 2, SWS, and REM in relation to time spent in bed, and sleep efficiency index (time asleep per time in bed). Original learning was defined as the number of correct items on the last learning trial. Two measures of recall were assessed. The number of items given in the first recall trial adhered to the common single recall score. Extended recall on the other hand was measured by the cumulative count of correct responses over all of the four recall trials. That is, a correct response was scored once the first time it was produced while ignoring subsequent repetitions. Forgetting was then defined as the difference between the recall score and the original learning score divided by the original learning score. Multiplication by 100 yielded the percentage of items lost over the retention interval. Recognition performance was assessed by the number of correct choices (hits). Due to the application of forced-list recognition, no extra measure of response bias was necessary (45).

Pairwise Dunnett t tests (46), denoted t_d, for multiple comparisons with a single control (i.e. the sleep condition) were calculated for finger tapping rates, sleepiness ratings (two-tailed tests), percent loss scores, and recognition hits (one-tailed tests) to compare sleepiness and memory performance between the Wake/Day and Sleep/Night and the Wake/Night and Sleep/Night conditions respectively. Unless specified otherwise, all data presented in the Results section are expressed as means ± standard error of mean (SEM).

RESULTS

Sleep parameters and sleepiness

Sleep parameters in the experimental night (Table 1) were within the normal range of healthy young subjects (47-50) indicating successful realization of the sleep condition.

Table 1. Sleep parameters in the experimental night

Sleep parameter	Mean	SEM
Time in bed [min]	414.96	3.13
S2-Sleep onset latency [min]	19.17	2.98
Sleep efficiency	92.09	1.36
% Wake	7.89	1.36
% S1	9.28	1.16
% S2	41.21	1.46
% SWS	20.72	1.33
% REM	17.79	1.41
% MT	3.10	0.78

Note. S1: sleep stage 1; S2: sleep stage 2; SWS: slow wave sleep; REM: rapid eye movement sleep; MT: movement time. Percentages are relative to time in bed.

Finger tapping rates (Figure 1A) did not indicate substantial differences between conditions at learning (Wake/Day: 302.88±9.85; Sleep/Night: 300.00±17.44; Wake/Night: 316.50±13.18; t_d(37)= 0.16 for comparison Wake/Day vs. Sleep/Night and t_d (37)=0.83 for comparison Wake/Night vs. Sleep/Night) and recall (Wake/Day: 306.31±11.50; Sleep/Night: 302.58±14.41;

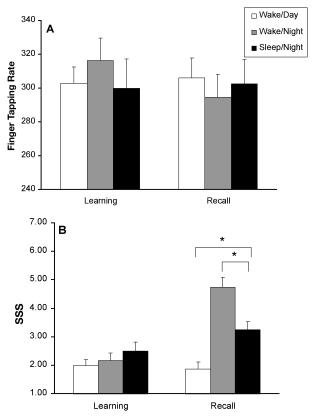


Figure 1. Control variables at learning and recall for the three experimental conditions. A Finger tapping rates (M \pm SEM). B Ratings on the Stanford Sleepiness Scale (M \pm SEM).

Wake/Night: 294.67 ± 13.71 ; $t_d(37)=0.20$ for comparison Wake/Day vs. Sleep/Night; t_d (37)= 0.41 for comparison Wake/Night vs. Sleep/Night). Subjective sleepiness ratings (Figure 1B) were comparable at learning (Wake/Day: 2.00±0.20; Sleep/Night: 2.50± 0.31; Wake/Night: 2.17 ± 0.27 ; t_d (37)= 1.39; p= .14 for comparison Wake/Day vs. Sleep/Night; t_d (22)= 0.87 for comparison Wake/Night vs. Sleep/Night) but showed considerable differences at recall (Wake/Day: 1.88±0.24; Sleep/Night: 3.25±0.28; Wake/ Night: 4.75 ± 0.35 ; t_d (37)= 3.45; p= .002 for comparison Wake/Day vs. Sleep/Night; td (37)= 3.52; p= .001 for comparison Wake/ Night vs. Sleep/Night).

Memory measures

Figure 2 illustrates the number of items recalled in the paired-associate task at three different stages of memory testing: (i) the last test trial during learning, which marks the original learning score (OL), (ii) the first test trial during recall (T1), and (iii) the last test trial during recall, which is expressed as cumulative score over all test trials (T1-T4 cum.). Levels of original learning were 9.69±0.73 for the Wake/Day, 10.67±1.07 for the Wake/Night, and 10.00±0.83 for the Sleep/Night condition. Between the last learning trial and the first recall trial, memory performance declined markedly

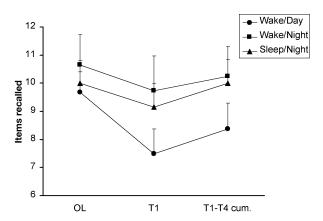


Figure 2. Number of items recalled on the last learning trial (OL), the first recall trial after the 7 h retention interval (T1), and cumulatively across all four consecutive recall trials (T1-T4 cum.). Error bars indicate SEM.

in the Wake/Day condition (2.12±0.54 items lost) and to a lesser extent in the two night conditions (Wake/Night: 0.92±0.26; Sleep/Night: 0.83±0.39 items lost). However, forgetting was alleviated during successive recall in all groups, which led to a recovery of 9.97%±2.68% (Wake/Day), 8.19%±4.13% (Wake/Night), and 8.09%±3.66% (Sleep/Night) of the items originally not recalled on T1

Proportions of items lost over the retention interval are shown in Figure 3 for T1 and T1-T4 cum. The main finding holds for both measures: subjects in the Wake/Day condition lost substantially more items (T1: 25.89%±7.21%; T1-T4 cum.: 15.92%± 6.86%) than did subjects in the Sleep/Night condition (T1: 7.58%±4.19%; T1-T4 cum.: -0.52%±3.82%) yielding test statistics of $t_d(37)$ = 2.19 (p= .031) for T1 and $t_d(37)$ = 2.09 (p= .039) for T1-T4 cum. However, subjects in the Wake/Night condition (T1: 11.98%±4.67%; T1-T4 cum.: 3.79%±4.35%) did not loose significantly more items than those in the Sleep/Night condition (T1: t_d (37)= 0.49; T1-T4 cum.: $t_d(37)$ = 0.51).

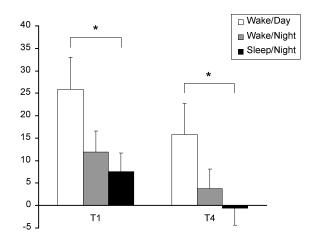


Figure 3. Percentage of items lost between original learning and the first recall trial (T1) and between original learning and the last recall trial (T1-T4 cum.). Scores at T1-T4 cum. are cumulative across all four consecutive recall trials. Error bars indicate SEM.

The number of recognition hits was generally high under all conditions (Wake/Day: 13.31±0.60; Wake/Night: 14.08±0.40;

Sleep/Night: 14.00 ± 0.30). There were no substantial differences between groups for this measure (t_d (37)= 1,01; p= .25 for comparison Wake/Day vs. Sleep/Night, t_d (37)= 0.11; p= 0.70 for comparison Wake/Night vs. Sleep/Night).

DISCUSSION

In accordance with previous research, the results of the present study confirmed superior declarative retention after a period of night sleep in comparison to a period of daytime activity. Subjects in the Wake/Day condition lost one-fourth of list associations on the first recall attempt and still 16% after cumulating over all recall trials while those in the Sleep/Night condition in fact showed a minimal increase (0.52%) of items or negative forgetting in the cumulative count. Based on the assumption that this effect is due to sleep per se, it was predicted that night sleep would also lead to better memory performance when compared to a condition of nightly waking activity. However, our data do not corroborate this hypothesis. Retention did not differ significantly between the two night conditions. This result is even more remarkable in view of the sleepiness data we obtained. While ratings of subjective sleepiness did not differ at learning, subjects in the Wake/Night condition exhibited the expected dramatic rise in sleepiness over night. On the average, they felt "foggy, losing interest in remaining awake" whereas subjects in the Sleep/Night condition were "awake, but relaxed; responsive but not fully alert" and those in the Wake/Day condition were "functioning at high level, but not at peak; able to concentrate". Thus, despite the fact that subjects in the sleep deprivation group acted at levels of severe drowsiness, they exhibited recall levels comparable to those in the sleep condition.

The application of successive recall trials in conjunction with guessing instructions from the second recall trial led to an improvement of memory performance in all groups. To what extent this partial recovery of items is related to one or the other factor cannot be determined and was not an aim of the present study. While we replicated the important finding, that a single recall trial is an insufficient measure of memory, there was no indication of a differential benefit between groups due to repeated recall. All groups recovered about 8-10% of the items so that the ranking of group performances was not affected by the extended recall procedure. Recognition performance did not differ significantly between groups albeit the ranking of group performances was the same as for recall.

With the present investigation we attempted to assess the effect of sleep on memory under various methodological precautions including application of pairedassociate learning, which is known to be sensitive for the effect of sleep; exhaustion of long-term storage by extended recall; Wake/Day control group to replicate previous results; polysomnographic control of night sleep; separate accomplishment of sleep deprivation to prevent exchange of material between learning subjects. Notwithstanding these strict methodologies, our results were negative with regard to a sleep memory effect under conditions of circadian phasing, as were those obtained by Nesca and Koulack (6). It should be noted that the effect of sleep on retention of pair associations is usually strong enough to prove statistically valid with 10-16 subjects per condition (3), even when the retention interval covers only the first half of the night (12,13,15,17). Thus, although generally no direct conclusion can be drawn from a null result, our findings may put some constraints on the generalizability of the beneficial effect of sleep on retention.

The comparable retention levels under both night conditions cannot easily be reconciled with the results obtained by Idzikowski (19) who found a large effect on retention of sleep per se. It is however in line with the findings of Hockey et al. (18) and Nesca & Koulack (6). An apparent explanation for the non-difference between the two night conditions in these studies and in ours could be that circadian factors rather than sleep play a major role in controlling what is retained in long-term memory and what is not. Above all, the glucocorticoid cortisol seems the best candidate to mediate circadian fluctuations of performance. It has a well-established detrimental effect on the declarative (hippocampus-mediated) memory system (51-55) while its secretion follows a pronounced circadian rhythmicity with its

nadir in the first and its peak in the second half of the night (56,57). However, our results cannot readily be explained by the action of cortisol since experimental evidence indicates an increase of cortisol levels under conditions of sleep deprivation as opposed to nocturnal sleep (58,59). This increase should have led to a reduction of memory performance in the Wake/Night group, which we did not observe. The comparable levels of retention under both night conditions would be best explained by a factor that solely depends on circadian timing, but not on sleep. To our knowledge, empirical evidence for such a factor is yet outstanding.

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Appendix: Paired-associate list and recognition lures for response words (English translation in parentheses)

Stimulus	Response	Distractor
Beweis (proof)	Wirkung (effect)	Ergebnis (result)
Verein (club)	Beginn (beginning)	Anfang (origin)
Stimmung (mood)	Auswahl (choice)	Teilmenge (subset)
Geschöpf (creature)	Interesse (interest)	Gefallen (favour)
Antwort (answer)	Vertreter (agent)	Ersatzmann (substitute)
Haltung (attitude)	Beitrag (contribution)	Mitwirkung (participation)
Ferne (distance)	Inhalt (content)	Begriff (idea)
Aufgabe (task)	Richtung (direction)	Ziel (target)
Kosten (costs)	Geruch (smell)	Duft (fragrance)
Neffe (nephew)	Besitz (possession)	Eigentum (property)
Versuch (attempt)	Gebet (prayer)	Andacht (devotion)
Beruf (profession)	Monat (month)	Jahr (year)
Merkmal (characteristic)	Vortrag (lecture)	Rede (speech)
Bewohner (resident)	Kreislauf (circulation)	Umdrehung (rotation)
Profil (profile)	Gruppe (group)	Familie (family)
Gedicht (poem)	Wache (guard)	Aufsicht (supervision)