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Effects of Daytime Sleep on the Consolidation of Declarative Memory in Humans

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The effects of daytime sleep consisting exclusively of non-REM (NREM) sleep on the consolidation of declarative memory and overall functional status were studied in humans. In addition, the effects of daytime sleep on memory were studied in relation to the level of fixation of assimilated information. At the beginning of each experiment, the subject was given a declarative memory task: to remember 60 semantically unrelated pairs of words, 30 of which were memorized once and 30 twice; at the end of the experiment, the level of memory fixation was assessed. Each subject took part in two experiments: a test protocol, in which training was followed by sleep, and a control protocol, in which a video was watched instead of sleeping. The results showed that daytime sleep facilitated the reproduction of declarative memory, with improvements in the remembering of the 30 pairs of words memorized once but not in remembering the 30 pairs of words memorized twice. The dynamics of a simple sensorimotor reaction and subjective assessments of wellbeing, activity, and mood with and without sleep were similar, and there were no significant differences between the two types of experiment.

KEYWORDS: daytime sleep, learning, declarative memory, non-REM sleep, functional state.

The concept of memory consolidation generally refers to processes which, after some period of time and in the absence of further training, make memories stable to interference from competing or degrading factors [14]. In other words, memory becomes more stable. Studies in recent years have widened he concept of consolidation. In particular, consolidation can not only stabilize memory, but can also improve it [27]. The stabilizing phase of consolidation has been shown generally to occur during waking [28]. The improving phase of consolidation is linked particularly if not exclusively with sleep: recovery of previously lost memories during sleep has been demonstrated [6], as well as reinforcement after sleep, without further training, of skills acquired the previous day [9, 24]. Thus, consolidation probably includes at least two different phases of processing memory traces, each phase requiring a particular brain state, such as waking or sleep, or even particular phases of sleep [24, 27, 28].

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There is as yet no single accepted view regarding which concrete processes underlie memory consolidation. It remains unclear which mechanisms support the effects of sleep on memory. There are two main theories explaining the effects of sleep on different memory systems. According to the first [19, 20], the different phases (NREM or slow-wave sleep and REM or paradoxical sleep) and stages (stages 1–4 of NREM) of sleep have different effects on memory traces depending on which systems they belong to. This relates particularly to the deep stages of sleep – stages 3 and 4, or delta sleep, which dominate during the first hours of the night, and REM sleep, which dominates during the last hours of the night. Delta sleep is associated with the consolidation of information in the declarative memory system, while consolidation of non-declarative information depends on REM sleep. In particular, comparison of the reproduction of learned information after the first 3–4 h of nocturnal sleep with reproduction after the first 3–4 h shows that early sleep promotes the memorization of declarative information, while late sleep improves performance in tasks requiring the involvement of procedural memory [19].

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The second theory emphasizes the importance of the correct alternation of NREM and REM sleep for consolidation processes [10], i.e., both phases of sleep are obligatory for consolidation regardless of the memory trace system concerned. Form this point of view, NREM and REM sleep supplement each other, while the sequence of sleep stages reflects different stages in the conversion of a labile memory trace into a more stable and long-lasting form. These two theories do not contradict each other, even if both sleep phases, NREM and REM, are involved in consolidation of a concrete type of memory and one phase or stage of sleep is more important than the others.

Declarative memory, whose formation requires involvement of the hippocampus and structures in the medial temporal areas of the hemispheres, consists mainly of memories for events and facts. A number of studies have shown that NREM sleep is the most important for consolidation of this type of memory [19, 20]. Furthermore, data evidencing that learning requiring the involvement of declarative memory in turn affects subsequent slow-wave sleep has been obtained. In particular, it has been demonstrated that performing tasks based on remembering declarative information leads to increases in the number of sleep spindles during subsequent sleep [8], along with increases in the coherence of slow-wave activity in the polysomnogram [16]. Thus, learning based on declarative memory affects the electrophysiological correlates of the slow-wave phase of sleep. This effect is most marked at the beginning of the night, during the first 90 min of sleep [8].

What actually mediates the positive effect of sleep on the consolidation of declarative memory remains unclear. The early hours of the night are characterized by the lowest levels of the stress hormone cortisol in the blood. The blood concentration of the stress hormone cortisol at the beginning of the night is at its lowest level and injections of cortisol at this time do not lead to sleep having positive effects on remembering pairs of words [21]. In addition, the early part of the night also shows the lowest levels of acetylcholine; cholinesterase inhibitors, which increase acetylcholine contents, are known to block consolidation [7]. Other studies have identified a positive correlation between the volume of reproduction of information learned the previous day and the extent of sleep spindles during nocturnal sleep seen after training [4]. Some authors believe that the role of sleep in memory processes is exclusively passive and that the favorable effects of sleep on memory are explained solely by the absence of interfering stimuli during the deep stages of sleep [29]. Nonetheless, the authors of [18] showed that progress in hippocampus-dependent spatial memory (remembering routes on a virtual road) after nocturnal sleep correlated positively with the level of activation of the hippocampus during slow-wave sleep. These data indicate an active role for sleep in memory consolidation processes.

However, significant disadvantages of studies addressing the influences of individual phases of nocturnal sleep on memory are that early nocturnal sleep includes some number of REM phases and that slow-wave sleep can occur in the pre-morning hours. In addition, in a number of nocturnal studies [5, 19, 20], the control groups were subjected to partial or complete sleep deprivation, which could not fail to be reflected in the subjects' ability to function. In other studies [11, 24], deprivation was avoided by performing training and memory tested in the experimental and control groups at different times of day: for example, the control ("non-sleeping") group was trained in the morning and testing in the late evening, the opposite timings being used in the "sleeping" group. Overall, the study results were influenced either by stress evoked by sleep deprivation or the circadian factor.

From this point of view, daytime sleep is a more convenient experimental model; furthermore, brief periods of daytime sleep generally include only stages 1–4, without a REM phase, thus allowing the effects of exclusively NREM sleep to be studied.

Investigations addressing the effects of daytime sleep on declarative memory are few and their results are ambiguous. Studies of the effects of daytime sleep on remembering 40 pairs of words were reported in [1] and [25]. However, while the latter study revealed a statistically significant positive effect of sleep on declarative memory, the former found no differences between the waking and sleeping groups in the reproduction of learned pairs of words. One of the reasons for this dissimilarity in results may be the different quantity of slow-wave sleep: with essentially identical sleep durations in subjects in the experiments reported in [1], deep sleep (stages 3 and 4) lasted a group mean period of only 8.7 min, while slow-wave sleep occupied 22.4 min in [25]. Division of sleeping subjects into two groups depending on the depth of sleep and comparison of the level of memory fixation in subjects showing slow-wave sleep and subjects showing only sleep stage 2 in these two studies also gave different results. The authors of the first of these two studies observed better remembering in the group with deep sleep, while the authors of the second found no relationship between memory consolidation and the time spent in slow-wave sleep.

The studies of Lahl et al. [12] addressed the effects of the total duration of daytime sleep on verbal declarative memory. Remembering of 30 words was assessed after a 60-min break during which one group of subjects slept (long sleep); the other group also slept, but the subjects were woken after 6 min of sleep (short sleep); the third group remained awake. The results showed that the number of correctly reproduced words was significantly greater in subjects who slept, the best remembering being seen after long sleep, with rather worse, but nonetheless significantly better remembering in the group who slept for 6 min than in

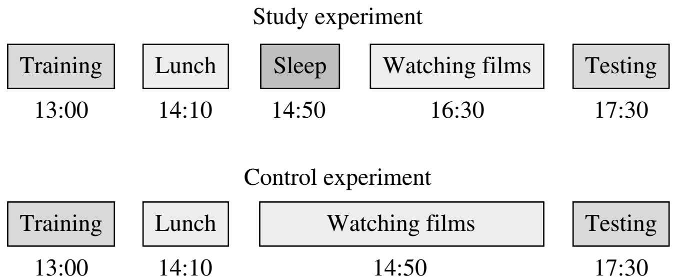

Fig. 1. Experimental protocol. For explanation see text.

subjects who remained awake. The authors concluded that the inclusion of sleep per se provided significant facilitation of consolidation.

However, data have also been obtained on the positive effect of daytime sleep on functional status and work capacity. In particular, Brooks and Lack [2] showed that short periods of daytime sleep of different durations (from 10 to 30 min) led to improvements in both wellbeing and cognitive functions: reaction times decreased and the stability of attention increased. As a small number of studies addressing the effects of daytime sleep on the consolidation of declarative memory did not follow changes in work capacity during the experiment, it was not entirely clear what determined the better remembering of information after sleep: facilitation of memory consolidation or merely the improvement in general functional status.

There is also the view that the effects of sleep on declarative memory may depend on the method of teaching the information and individual learning success. Studies reported in [26] noted positive effects of sleep on remembering pairs of words only in those subjects who "learned well" – these gave the best results during training. In addition, sleep improved the reproduction of those pairs of words which were learned best during training. There are also directly contradictory data on the effects of sleep on memory traces with different levels of fixation. In particular, experiments reported in [5] showed that sleep improved the reproduction only of weak memory traces – information learned less well or subjected to interference by competing events immediately after learning.

The aim of the present work was to study the effects of daytime sleep not only on the consolidation of declarative memory, but also on work capacity and overall functional status in humans: if improved reproduction of learned material is seen after sleep on the background of an improved functional status, this would indicate more an effect of sleep on work capacity than an effect of sleep on memory. We also assessed whether the effect of sleep on memory depends on the level of "learning" of the material (two memorizations or one memorization) and whether the effect of sleep on memory depends on the depth and duration of sleep.

METHODS

A total of 14 subjects aged from 20 to 40 years (six women, eight men) took part in the study. Each subject took part in two protocols: a study experiment and a control experiment. The experimental schemes are shown in Fig. 1. At the beginning of each experiment, at 13:00, subjects were given a memory task requiring the involvement of declarative memory; at the end of the experiment, the level of fixation of memory was assessed. In the study experiment, training was followed by lunch, after which the subjects slept for 1 h in a soundproofed room. From the moment of waking to final testing of the fixation of the remembered material, the subjects watched a nature video (any two episodes of a collection of 11 episodes of the BBC documentary "Planet Earth"). Watching a video was selected as a passive activity allowing control of the influx of new information which might interfere with the information received during the training process. Final testing was performed at 17:30, such that the training phase of the experiment and final testing were separated by 4.5 h. The control experiment differed from the study experiment only by lacking daytime sleep; subjects spent the whole period of time between lunch and final testing watching videos.

The interval between the study and control experiments was one week. Half the subjects started with the study experiment (with sleep) and progressed to the experiment without sleep one week later; the other half performed the experiment without sleep first and progressed to the experiment with sleep after one week.

We employed a test for declarative memory which is widely used in studies of this type [23] – the so-called word pair associations method. During training, a computer screen was used to present 60 semantically unconnected pairs of words, for example, crocodile–cigar. Each pair was displayed for 5 sec, with an interstimulus interval of 100 msec.

Testing and repeated memorization of 30 pairs was performed immediately after memorization of the 60 pairs of words, selected randomly from these 60: the first word of the pair was shown, the subject had to try to name the second word, and the correct word was then displayed. Thus,

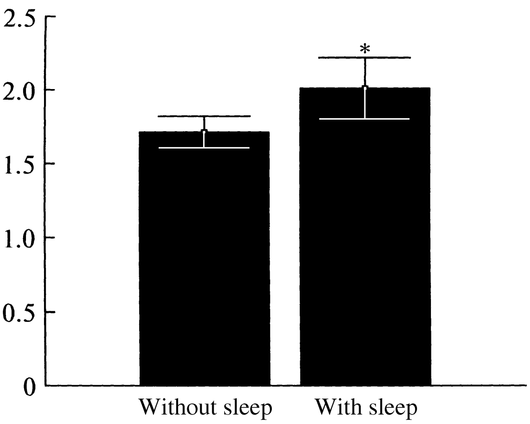

Fig. 2. Numbers of correct responses (arbitrary units), results of final testing of 60 pairs of words in the experiment without sleep and the experiment with sleep. The histogram shows errors of the mean. $^{*}p < 0.05$.

firstly, detailed testing of memory was performed during training and, secondly, half of the stimuli were presented twice for memorization.

At the end of the experiment, during final testing, the level of fixation of memory for all 60 pairs was assessed in random order: the first word of the pair was displayed and the subjects had to name the second. Apart from the results for all 60 pairs of words, the numbers of correct responses for the 30 pairs memorized twice and the 30 pairs of words memorized once were recorded. The results of final testing were normalized: the number of correct responses for all 60 pairs and the numbers of responses separately for the pairs memorized twice and once were divided by the result obtained on trial testing during training. This normalization was performed to minimize the effects of random factors (formation of the skill of memorizing unconnected pairs of words by the second experiment, variations in the level of the subjects' attention from experiment to experiment on the study results). Memorization tasks used different pairs of words in the two experiments.

Functional status at the learning and test stages of each experiment was evaluated by determining the simple sensorimotor reaction time and using the WAM questionnaire (wellbeing, activity, mood). The depth of sleep was assessed using a polysomnograph: recordings were made of the electrooculogram, the myogram of the mental muscles, and the EEG from six leads in the 10–20 system: F3, F4, C3, C4, O1, and O2. The reference electrode consisted of combined mastoid electrodes. These recordings were made using a PolySon multichannel computerized polygraph (Neirokom, Russia). The signal sampling frequency was 200 Hz. Sleep stages were identified using standard criteria [22] using a method blinded to test performance results.

Interactions between measures were evaluated using Pearson correlation matrixes and by assessment of the significance of intergroup differences, and changes in values from situation to situation were evaluated using the nonparametric Wilcoxon test for paired measurements. Statistical analysis was performed in Statistica for Windows 7.

RESULTS

Polysomnogram analysis showed that four subjects showed only shallow sleep (first and second stages), while 10 also showed deep sleep, with the third stage and in some (four subjects) even the fourth. None of the subjects showed the REM phase of sleep. The group mean total duration of sleep was 40.85 min, with mean durations of the first, second, third, and fourth stages of 10.46, 22.59, 7.92, and 4.23 min, respectively; the mean duration of delta sleep (third + fourth stages) was 9.61 min.

Mean results from trial testing immediately after training showed that of the 30 pairs of words, subjects correctly named 15.43 pairs in the experiment without sleep and 13.29 pairs in the experiment with sleep, the difference between the two types of experiment being insignificant.

Mean results for final testing showed that of the 60 pairs of words at the end of the experiment without sleep, subjects correctly reproduced 25.29 pairs, compared with 23.79 pairs at the end of the experiment with sleep. Significant differences between the two types of experiment were seen for the results of final testing normalized with respect to the results of trial testing: at the end of the experiment with sleep, subjects correctly reproduced significantly more pairs of words than in the experiment without sleep, at $p < 0.047$ (Fig. 2).

The numbers of correct responses were then analyzed for pairs of words with different numbers of memorizations. Of the 30 pairs of words memorized twice, 18.85 pairs were correctly reproduced at the end of the experiment without sleep, compared with 16.71 at the end of the experiment with sleep; of the 30 pairs of words memorized once, 6.42 were correctly reproduced without sleep, compared with 7.07 pairs after sleep. For pairs of words memorized twice, no significant differences were seen between the experiments (Fig. 3, *A*). Significant differences between the two types of experiment were seen for normalized values for the 30 pairs memorized once: at the end of the experiment with sleep, subjects correctly reproduced significantly more pairs of words than in the experiment without sleep, $p < 0.035$ (Fig. 3, *B*).

Correlation analysis was performed between total sleep duration, the durations of the four stages of sleep, the duration of delta sleep (stages 3 + 4), and the number of correctly reproduced pairs of words at the end of the experiment with daytime sleep. However, no significant correlational relationships between sleep measures and the numbers of correct responses were seen.

Data from the WAM questionnaire were used to analyze subjective assessments of functional status at the train-

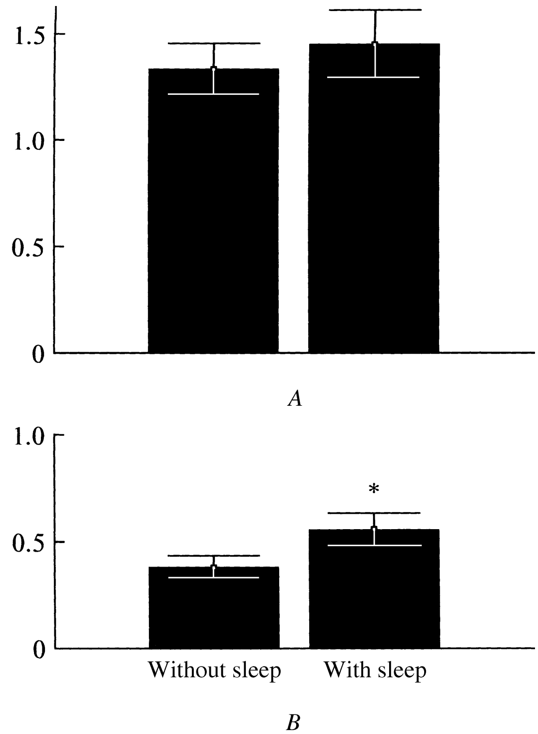

Fig. 3. Numbers of correct responses (arbitrary units), results of final testing of 60 pairs of words in the experiment without sleep and the experiment with sleep. *A*) For 30 pairs of words memorized twice during training; *B*) for 30 pairs of words memorized once during training. For details see caption to Fig. 2.

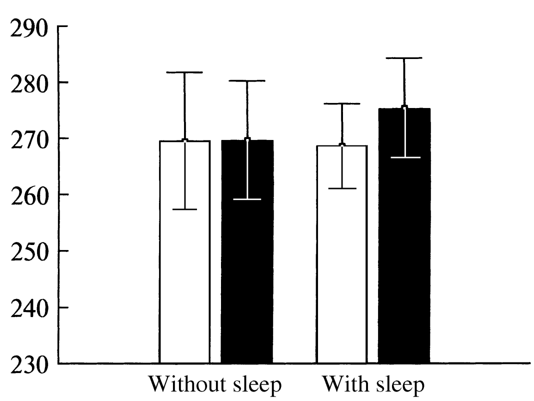

Fig. 4. Simple sensorimotor reaction times during training (gray columns) and during testing (black columns) in the experiment without sleep and the experiment with sleep.

ing and test stages of each experiment. Significant changes in functional status were not seen either during the experiments with sleep or during the experiments without sleep. WAM score differences between the two types of experiment were also insignificant.

Simple sensorimotor reaction times (Fig. 4) by the end of the experiment with sleep increased slightly, though this change was not significant. There were also no significant differences between the two types of experiment.

DISCUSSION

The results obtained here show that daytime sleep following training and consisting only of the slow-wave phase facilitated the remembering of declarative information. Sleep promoted learning of the 30 pairs of words memorized once but had no effect on the reproduction of the 30 pairs of words memorized twice.

The dynamics of the simple sensorimotor reaction time and subject assessments of wellbeing, activity, and mood in experiments with and without sleep were similar, and there were no significant differences between the two types of experiment. This leads to the conclusion that the better memorization in experiments with sleep could not be explained only by the influence of sleep on functional status.

Published data provide evidence that slow-wave sleep can produce a state in which fresh memory traces stored temporarily in the hippocampus are transferred to the neocortex for integration into long-term memory [3, 15]. Sleep is believed to facilitate memory consolidation by cryptic reactivation of recently formed images [13, 15]. In particular, during the process of formation of declarative memory, which is closely associated with the operation of the hippocampus, during slow-wave sleep following the training session, reactivation of those populations of hippocampal neurons which were active during training has been demonstrated [17, 18]. Thus, the concept of the active role of sleep in memory consolidation is based on the fact that reactivation of those neuronal ensembles which took part in perception occurs during sleep. In other words, this is an analog of repeated playback of information received while awake. It may be that in our experiments, this repetition was critical for words presented once during training but was not needed for words memorized twice. Ultimately, sleep affected the reproduction of weak memory traces – only those words memorized once.

However, as we did not find significant links between improvements in the reproduction of memorized pairs after sleep and the characteristics of that sleep, we cannot take the view that sleep had active influences on the remembering of information in our experiments. However, the absence of significant correlations may be because our cohort was heterogeneous in terms of sleep quality: deep sleep (stages 3 and 4) was not recorded in some subjects. Our further intention is to analyze relationships between the depth and duration of sleep and its effects on memory separately for deep and superficial (stages 1 and 2) sleep.

It has also been suggested that the effects of sleep on memory may depend on the subjects' level of success in acquiring the task [11, 26] and the method of memorizing information [26]. In particular, it has been shown in the case of motor memory that better assimilation of motor tasks during training is accompanied by significant increases in slow activity during subsequent sleep, and this increase in slow activity in turn correlated with the extent of improvements in task performance after sleep [11]. In [26], marked progress in performing declarative memory tasks after sleep was seen only in "stars" – those subjects who produced the best results on learning. Thus, individual success in acquiring tasks may be a further factor affecting sleep-dependent memory consolidation. Furthermore, Tucker and Fishbein, using memorization of semantically unrelated pairs of words, demonstrated a significant effect of sleep for those pairs of words for which the best memorization conditions were created [26]. In this study, all pairs of words were presented for memorization twice during training, though some of them were tested after the first memorization, which improved the level of fixation of their assimilation.

Our results do not support these views. However, a different experimental protocol was used in the present studies: half of the material for memorization was presented once (i.e., conditions for memorization were worse than those for the untested pairs in [26]), and half were tested during training with immediate display of the correct response (so the conditions for memorization were better than for the pairs tested in [26]). The difference in the results may be due to differences in the memorization tasks. It should be noted that the inclusion of intermediate testing during training influences assimilation of information and that in this situation the process of memorization may be qualitatively different from that in passive memorization without "checking."

Ultimately, our data support the results obtained in [5], which showed that sleep improves the reproduction of weak memory traces which were learned worse or were impaired by interference, but does not influence the memorization of well assimilated information. The authors of [5] believe that this selective influence of sleep on memory is evidence for its active role in consolidation. If the role of sleep were passive and restricted to protecting fresh and therefore fragile memory traces from interference, then, according to these authors, the reproduction of all the material – both well memorized and poorly memorized – would improve to the same extent.

CONCLUSIONS

1. Daytime sleep following training and consisting only on the slow-wave phase facilitated the reproduction of declarative information.

2. Sleep promoted the reproduction of information memorized once but had no effect on the reproduction of information memorized twice.

3. The dynamics of simple sensorimotor reaction time and subject assessments of welling, activity, and mood in experiments with and without sleep were similar, and there were no significant differences between the two types of experiment. This leads to the conclusion that better memorization in experiments with sleep cannot be explained only by the effects of sleep on functional state.

4. Correlation analysis between the level of fixation of memory and sleep characteristics – total sleep duration and the durations of separate phases – did not identify any significant correlations between sleep quality and its effect on learning.

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