Consolidation of Strictly Episodic Memories Mainly Requires Rapid Eye Movement Sleep

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Study objectives: The aim of this study is to examine the effects of sleep deprivation during the first or second half of the night on episodic memory consolidation. *Episodic memory* is defined as memory for events located in time and space. It is also characterized by autonoetic consciousness, which gives a subject the conscious sensation of traveling back in time to relive the original event and forward into the future.

Design: Consolidation of episodic information was tested after 4-hour retention intervals, which followed learning and occurred during either the early or late half night, respectively dominated by slow wave sleep (SWS) or rapid eye movement (REM) sleep, or corresponding periods of wakefulness.

Setting: Data collection occurred in the sleep laboratory.

Participants: Forty-three young healthy subjects: 9 men and 34 women, age ranging from 18 to 26 years (mean 20.18 ± 1.94 years) were included in this study.

Interventions: Waking after a 4-hour retention interval filled with early or late sleep, or 4-hour sleep deprivation, during early or late period of night.

Measurements and Results: The cognitive task, named the What-Where-When test, was specially designed to assess factual, spatial, and temporal components of episodic memory. This task was associated with the Remember/Know paradigm to assess autonoetic consciousness. We measured performance on immediate free recall, delayed free recall (after a 4-hour interval of wakefulness or sleep), and delayed recognition. We also calculated a forgetting rate for each feature (factual, spatial, and temporal) and, for the recognition task, scores of autonoetic consciousness (R responses). REM-sleep deprivation was associated with significantly lower recall of spatial information compared to SWS deprivation ($P < .01$) or late sleep ($P < .05$) conditions. REM-sleep deprivation was also associated with a higher forgetting rate of temporal information as compared to the early sleep condition ($P < .01$). Finally, REM-sleep deprivation led subjects to give significantly fewer R responses, indicative of true memories, as compared to SWS deprivation ($P < .05$).

Conclusions: These results suggest that consolidation of truly episodic memories mainly involves REM sleep.

Keywords: Sleep deprivation; slow-wave sleep; REM sleep; episodic memory; memory consolidation; autonoetic consciousness.

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INTRODUCTION

NUMEROUS STUDIES SUGGEST THAT SLEEP IS INVOLVED IN MEMORY CONSOLIDATION, DEFINED AS THE TIME-DEPENDENT PROCESS THAT CONVERTS LABILE MEMORY TRACES INTO MORE PERMANENT FORMS. Memory is not a unitary cognitive function but is composed of several subsystems, subserved by different brain structures.[1,2] Episodic memory refers to a system that stores events located in time and space and implicates a conscious recollection of these experiences.[1,3,4] In contrast, implicit memory refers to the nonconscious influence of previous experiences on subsequent performance in tasks that do not require the intentional recollection of these experiments.[5] A large body of evidence indicates that slow-wave sleep (SWS) and rapid eye movement (REM) sleep act differentially on memory traces belonging to different memory subsystems (see [6] for review). According to this view, SWS would improve consolidation of episodic memories, whereas REM sleep would enhance consolidation of implicit ones. Indeed, episodic recall of paired-associate word lists improves more after the first half of a night's sleep (early sleep), dominated by SWS, than after the second half (late sleep), dominated by REM sleep

(7 and 6,8 for reviews). As for implicit tasks, Plihal and Born[7] have shown that mirror-tracing skills improve more after REM sleep than after SWS. Likewise, Karni et al[9] found that selective REM-sleep deprivation abolishes overnight improvement on a visual discrimination task. These results are consistent with neuroimaging data indicating that several brain areas activated during a serial reaction time task were reactivated during REM sleep in subjects trained to this task.[10]

However, the results of some studies do not support the SWS/episodic memory and REM sleep/implicit memory dichotomy and seem to suggest that the relationship between sleep stages and different memory types is more complex. Indeed, recall of sentences, prose passages, or short stories, though generally categorized as episodic-memory tasks, is impaired after selective REM-sleep deprivation (see [6] for review). Emotional-material retention also appears to depend on REM sleep. Wagner et al[11] compared memory retention of neutral and emotional texts and found that memory for emotional text was enhanced by REM sleep. This result was indirectly confirmed by neuroimaging data revealing activation of the amygdala, a structure known to be involved in the processing of emotions, during REM sleep.[12] Moreover, using exactly the same task and sleep-deprivation paradigm as Karni et al,[9] Gais et al[13] found that visual-discrimination skills were enhanced after SWS. REM sleep may also promote implicit-memory formation but only at a second stage, once SWS-related processes have occurred. In this vein, Stickgold et al[14] have shown that overnight improvement on this same task was correlated with both the amount of SWS in the first quarter of the night and the amount of REM sleep in the late quarter of the night. These data support the idea that memories acquired during wakefulness are processed during sleep in 2 sequential steps, occurring during SWS and REM sleep, respectively.[15]

In sum, the respective roles of SWS and REM sleep with regard to the consolidation of episodic and implicit memories are not clearly under-

stood. One possible explanation for the discrepant results could be the use of nonspecific tasks. Thus, the tasks used to assess episodic memory often do not truly fit the current definition of this memory system. Episodic memory refers to a system that stores events located in time and space and is characterized by autonoetic consciousness, which gives a subject the conscious sensation of traveling back in time to relive the original event and thus provides a mean of linking events in the past, present and future.[1,4] Autonoetic consciousness allows an individual to recollect vivid spatiotemporal and phenomenologic details of the previous event. This state of consciousness contrasts with noetic consciousness, which is characteristic of semantic memory and refers to a feeling of familiarity or knowledge without conscious recollection of events. These 2 kinds of mental experience are usually assessed during recognition tasks associated with the R/K paradigm.[16,17] "Remember" responses reflect autonoetic consciousness (episodic memory), while "Know" responses are based on a feeling of familiarity and reflect noetic consciousness (semantic memory). This paradigm has been used in numerous studies investigating episodic memories: in child development,[18] normal aging,[19] amnesic syndrome,[20] and neurodegenerative diseases such as Alzheimer disease[21] and frontotemporal dementia.[22]

The tasks used to assess episodic memory in sleep studies are generally restricted to learning lists of words. The different components of episodic memory (factual, spatial, and temporal) are rarely dissociated, and the state of consciousness is given little consideration. Only one recent study[23] has taken some of these points into account in an investigation of dreams. Fosse et al[23] examined the relationships between dreaming and episodic events that occurred during recent waking life. A replay of waking events was found in less than 2% of the dreams reported, leading the authors to conclude that sleep plays no role in episodic-memory consolidation, inconsistent with Plihal and Born's conclusions. Thus, until now, no study has assessed the effect of sleep stages on the consolidation of purely episodic information.

In light of such conflicting results concerning the relationship between sleep and memory, the purpose of the present study was to examine the effects of SWS or REM-sleep deprivation on episodic-memory consolidation, using an original task that takes into account the 3 components (factual, spatial, and temporal) of episodic memory, as well as the state of consciousness of the subject performing the task.

MATERIAL AND METHODS

Subjects

A total of 61 subjects, aged 18 to 27 years, participated in this study. They were asked to fill out a questionnaire about their sleep patterns and lifestyle. Subjects who had unusual sleep habits (such as very late bedtimes) or a history of sleep disturbances, who took medication, or who claimed to smoke (more than 10 cigarettes per day) or drink excessively (regular consumption of alcohol) were excluded from this study. Two criteria of a posteriori exclusion were added: subjects presenting a sleep efficiency (defined as the ratio between total sleep time and total sleep period) lower than 85% or a majority of REM sleep during the first-half night or, conversely, second-half night with predominant SWS, were excluded from this study. Finally, 43 subjects (9 men, 34 women), aged 18 to 26 years (mean 20.18 ± 1.94 years) were included. All subjects gave their consent to participate in the study after detailed information was provided to them, and the study was in accordance with the Declaration of Helsinki.
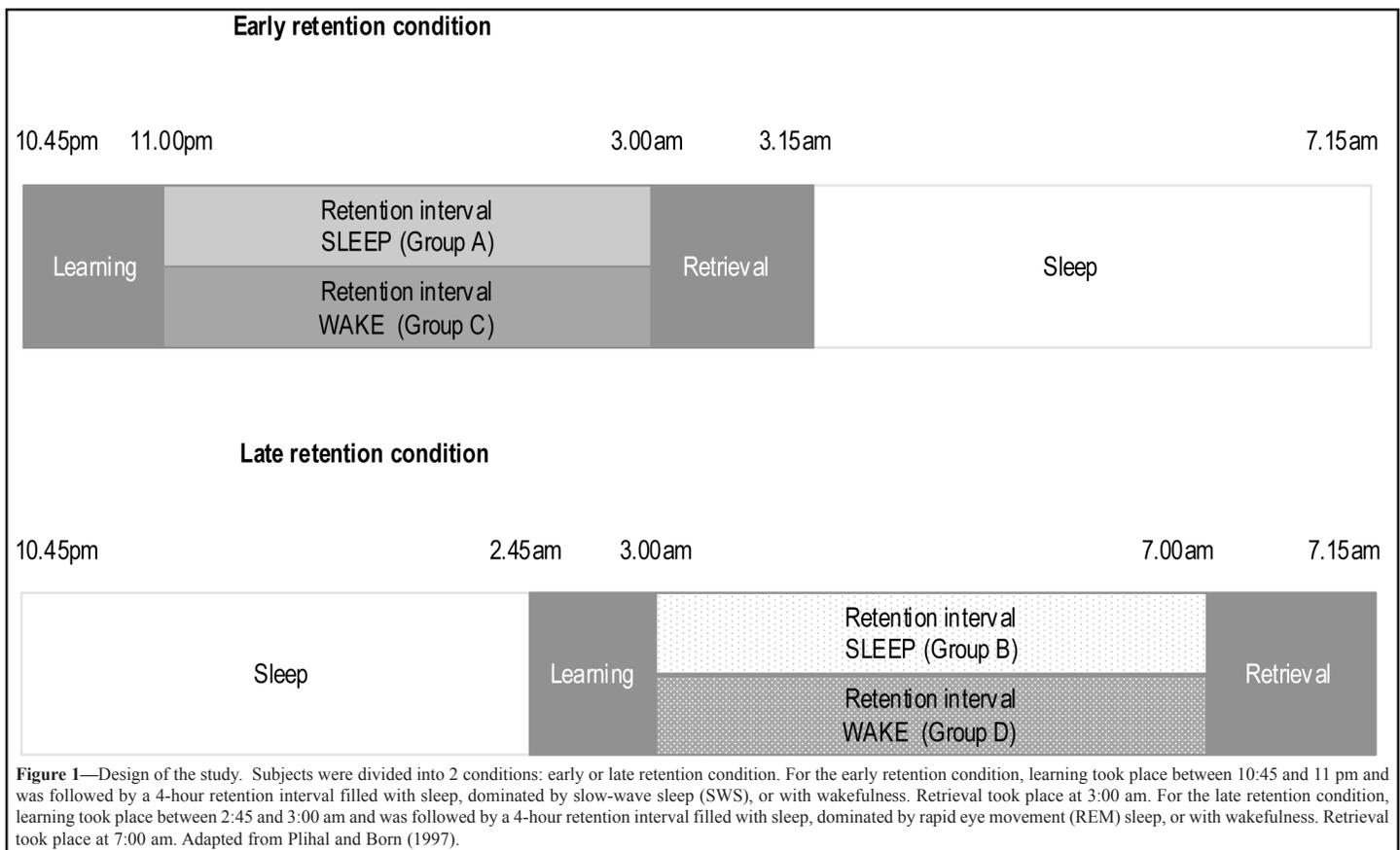
Design and Procedure

Figure 1 illustrates the design of the study. The experiment took place in the sleep laboratory of the University Hospital of Caen. The procedure followed in this study was similar to that described by Plihal and Born.[7] Subjects were divided into 4 groups.

Sleep Groups

Early Sleep Condition

Subjects (n = 11, 8 women and 3 men; group A) reported to the sleep laboratory at 7:30 PM and, after placement of electrodes for sleep

Figure 1—Design of the study. Subjects were divided into 2 conditions: early or late retention condition. For the early retention condition, learning took place between 10:45 and 11 pm and was followed by a 4-hour retention interval filled with sleep, dominated by slow-wave sleep (SWS), or with wakefulness. Retrieval took place at 3:00 am. For the late retention condition, learning took place between 2:45 and 3:00 am and was followed by a 4-hour retention interval filled with sleep, dominated by rapid eye movement (REM) sleep, or with wakefulness. Retrieval took place at 7:00 am. Adapted from Plihal and Born (1997).

recording, performed the first part of the task between 10:45 PM and 11:00 PM (see Memory testing section) and the second part after a 4-hour sleep interval, dominated by SWS. After testing, subjects slept until 7:00 AM.

Late Sleep Condition

After sleeping 4 hours, subjects (n = 9, all women; group B) performed the first part of the test between 2:45 AM and 3:00 AM, and the second part after a 4-hour sleep-retention interval dominated by REM sleep.

Wake Groups

Early sleep deprivation (n = 12, 9 women and 3 men; group C) and *Late sleep deprivation* (n = 11, 8 women and 3 men; group D). The procedure was exactly the same as for the corresponding sleep group, except that the 4-hour retention interval was filled with wakefulness instead of sleep. Wakefulness was not monitored with electroencephalography, but, to remain awake without too much cognitive or emotional strain, subjects were allowed to play games or watch television. These activities also prevented rehearsal of learned material.

A 15-minute interval was placed between awakening and learning, based on findings of Bonnet[24] indicating an impairing effect of prior sleep on learning and memory formation when learning takes place in the first 8 minutes after awakening.

Sleep Recording

Sleep was assessed by standard polysomnography, including electroencephalogram, electrooculogram, and electromyogram. Recordings were scored off line by an experienced neurologist according to the criteria of Rechtschaffen and Kales.[25] For each 4-hour interval, total sleep time, sleep-onset latency, sleep efficiency, and the time and percentage of time spent in sleep stages 1, 2, 3, 4, and REM were determined. Time spent in SWS was calculated by adding time spent in stages 3 and 4.

Memory Testing

The episodic task used in this study was derived from Kopelman's procedure and assesses the ability to learn facts associated with spatial and temporal features.[26] Although this test is not an ecologic evaluation of episodic memory, it proved to be sensitive to frontal dysfunctions characterized by a deterioration of temporal memory and to hippocampal alterations resulting in an impairment of spatial memory.[26] This task, adapted from the original What-Where-When test,[27] is illustrated in Figure 2. It comprised 2 lists of 7 words belonging to 14 different semantic categories, presented at the top or the bottom of a page. The first part of the task consisted of memorizing a word (factual information), its location (spatial information), and the list to which it belongs (temporal information). Immediately after subjects learned this information, free recall was tested. The second part of the task took place after a 4-hour retention interval, filled with early or late sleep or wakefulness, and comprised another free recall, followed by a forced choice recognition task for the word and each feature (spatial and temporal). During this
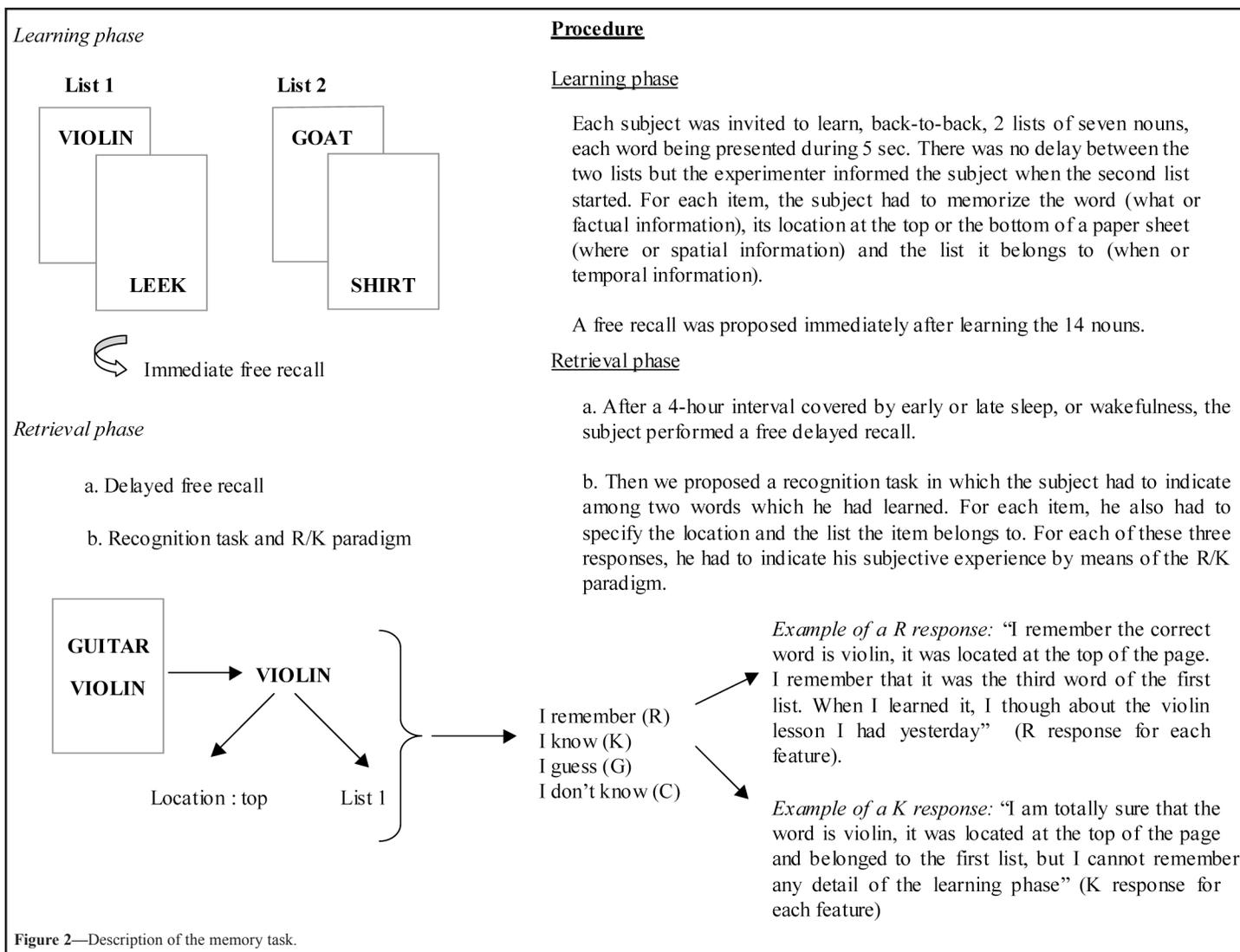

Learning phase

Procedure

List 1

VIOLIN

LEEK

List 2

GOAT

SHIRT

↩ Immediate free recall

Retrieval phase

a. Delayed free recall

b. Recognition task and R/K paradigm

GUITAR
VIOLIN → VIOLIN

Location : top   List 1

I remember (R)
I know (K)
I guess (G)
I don't know (C)

Learning phase

Each subject was invited to learn, back-to-back, 2 lists of seven nouns, each word being presented during 5 sec. There was no delay between the two lists but the experimenter informed the subject when the second list started. For each item, the subject had to memorize the word (what or factual information), its location at the top or the bottom of a paper sheet (where or spatial information) and the list it belongs to (when or temporal information).

A free recall was proposed immediately after learning the 14 nouns.

Retrieval phase

a. After a 4-hour interval covered by early or late sleep, or wakefulness, the subject performed a free delayed recall.

b. Then we proposed a recognition task in which the subject had to indicate among two words which he had learned. For each item, he also had to specify the location and the list the item belongs to. For each of these three responses, he had to indicate his subjective experience by means of the R/K paradigm.

Example of a R response: "I remember the correct word is violin, it was located at the top of the page. I remember that it was the third word of the first list. When I learned it, I though about the violin lesson I had yesterday" (R response for each feature).

Example of a K response: "I am totally sure that the word is violin, it was located at the top of the page and belonged to the first list, but I cannot remember any detail of the learning phase" (K response for each feature)

Figure 2—Description of the memory task.

recognition task, the subject had to also indicate for each response his or her subjective experience by means of the R (Remember, autonoetic consciousness) / K (Know, noetic consciousness) paradigm.[16] Standard instructions derived from Gardiner et al's study[28] were given and illustrated by a few examples. Thus, the subjects had to give either "Remember" responses (R) if they were able to bring to mind some recollection of what occurred when the item was encoded (ie, thoughts, feelings or perceptions, see Figure 2), or "Know" responses (K) if retrieval was achieved without such access. In addition, subjects lacking confidence in a response could indicate a vague feeling of familiarity with "Guess" (G) responses or complete uncertainty with "Chance" (C) responses.[29] Testing in this way ensured that R responses given by the subject actually reflected episodic memory.

We calculated a forgetting rate for the 3 components (factual, spatial, and temporal) from performance on immediate and delayed recall. For each feature, the formula was (performance on immediate free recall – performance on delayed free recall) / performance on immediate free recall. Spatial and temporal features were scored as correct responses only if factual information was exactly recalled and were then transformed into percentage correct relative to correct responses for factual information.

Concerning the recognition task, a first analysis was carried out using the percentage of correct recognition for factual, spatial, and temporal features. Spatial and temporal scores were again transformed into percentage correct relative to correct responses in factual recognition. Then, a second analysis was performed using the scores of subjective experience (R, K, G, and C responses), each score being transformed into percentage correct relative to correct responses in the 3 recognition tasks (factual, spatial, and temporal features). Only the strictly episodic responses (R responses), associated with correct factual, spatial, and temporal recognition, were used for the statistical analysis.

A Priori Hypotheses

We hypothesized that performance of the wake groups would be lower than that of the sleep groups, whatever the retention interval (ie, C: Early sleep deprivation < A: Early sleep; D: Late sleep deprivation < B: Late sleep) and the task (delayed recall or recognition) considered. Plihal and Born's works indicate that consolidation of episodic memory, assessed by recall of word lists, requires SWS. Consequently, we hypothesized that, for the factual component of episodic memory, performance would be better in the Early Sleep group (group A) than in the Late Sleep group (group B) and that SWS deprivation (group C) would impair consolidation more than REM-sleep deprivation (group D). Concerning spatial information, we hypothesized, according to the animal literature using spatial learning, a beneficial effect of REM sleep. On the other hand, we thought that SWS would be beneficial for retention of temporal information. Indeed, dreams mainly occur during REM sleep and are characterized by a temporal distortion. Hence, we thought that this sleep stage would not enhance consolidation of temporal information. Finally, concerning judgments, and particularly R responses, we hypothesized that activity occurring during REM sleep and dreaming, notably mental imagery and associative abilities, would favor the recollection of details about the encoding context, especially the spatial context.

In order to test these hypotheses, we performed the statistical analyses detailed in the following section.

Statistical Analyses

Sleep data recorded during the early and late sleep periods were compared using pairwise *t* tests. Statistical significance of neuropsychological data was assessed by analysis of variance (ANOVA), for each type of information, followed by posthoc tests (Fisher's PLSD) to determine the effect of the 2 factors "condition" (wake vs sleep) and "half night" (early vs late). In order to measure the magnitude of the effects, we also calculated the Cohen's d effect size[30] for all significant effects and trends reported. Cohen defined *d* as the difference between the means of 2

groups (M1-M2), divided by the SD of either group. In practice, the pooled SD, σ pooled, is commonly used.[31] The pooled SD is the square root of the average of the squared SDs (the root mean square). The formula is therefore $d = M_1 - M_2 / \sigma_{pooled}$. Cohen defined effect sizes as *small* when d is around 0.2, *medium* when d is around 0.5, and *large* if d exceeds 0.8.

RESULTS

Sleep Data

As expected, sleep architecture during the 2 half nights differed substantially with respect to SWS and REM sleep (see Table 1). SWS constituted about 37% of the early sleep interval but only 15% of the late one ($P < .0001$). In contrast, REM sleep constituted less than 10% of the early sleep interval and more than 26% of the late interval ($P < .0001$). Differences in the other sleep stages were not significant. Total sleep time was decreased in late sleep condition (early sleep: m = 203.4 ± 14.03 minutes; late sleep; m = 190.1 ± 18.2 minutes, $P < 0.01$), but sleep efficiencies between the 2 periods were not significantly different (95.7 ± 2.8 % vs 96.6 ± 2.1 %).

Neuropsychological Scores

Table 2 shows the results of all comparisons carried out. For scores on immediate free recall of factual information (see Figure 3a), the ANOVA did not reveal any simple effect of condition (wake vs sleep) ($P < .16$) or half night (early vs late) ($P < .94$). Similar results were obtained for immediate recall of spatial (condition: $P < .84$; half night: $P < .70$) and temporal information (condition: $P < .39$; half night: $P < .52$). Subjects performed similarly on immediate free recall regardless of when the learning session took place.

Analysis of the delayed free recall did not reveal any significant effect of condition or half night on recall of factual information. However, a significant interaction between condition and half night ($P < .01$) was found for recall of spatial information. Posthoc tests showed that subjects who were REM-sleep deprived (Late sleep deprivation, group D) recalled significantly less spatial information than subjects who slept during the late sleep interval (Late sleep, group B) ($P < .05$, Cohen's d = 1.15) (see Figure 3b). In addition, these REM-sleep-deprived subjects (group D) recalled significantly less spatial information than SWS-deprived subjects (Early sleep deprivation, group C) ($P < .01$, Cohen's d = 1.08). No significant differences were found for the delayed recall of temporal attributes.

For the forgetting rates, the ANOVA revealed a significant effect of half night ($P < .05$) only on the forgetting of temporal information. Subjects placed in the early retention condition, whether sleeping or awake, forgot fewer temporal attributes than did subjects placed in the late condition. The ANOVA did not reveal any significant interaction between these 2 factors (see Table 2). Nevertheless, posthoc analysis indicated a significant difference ($P < .01$, Cohen's d = 1.05) between

Table 1—Time* spent in each sleep stage during each experimental condition

Sleep Stage	Experimental Condition		*t*
	Early sleep	Late sleep	
Stage 1	20 ± 10.3 (9.2 ± 2.5)	21.5 ± 6.3 (11.5 ± 3)	-0.56
Stage 2	89.8 ± 17.8 (43.8 ± 7.2)	87.1 ± 19 (46.7 ± 10.8)	0.52
SWS	75.1 ± 13.3 (37 ± 7.4)	29.6 ± 11.6 (15.1 ± 6.1)	12.00‡
REM sleep	18.5 ± 8.5 (10 ± 5)	52.2 ± 15.5 (26.6 ± 7.5)	-10.67‡
Total sleep time	203.4 ± 14	190.1 ± 18.2	3.22†

*Time, in minutes, expressed as mean ± SD (mean ± SD percentage of total sleep time). spent in each sleep stage during early and late sleep.
SWS refers to slow-wave sleep; REM, rapid eye movement.
Results for statistical analysis by pairwise *t* test.
†*P* < .01
‡*P* < .0001

groups A and D and a trend ($P < .06$, Cohen's d = 0.78) between groups A and B (see Figure 3c). Subjects who slept during the SWS-dominated early half night (Early sleep: group A) tended to forget less temporal information than did subjects who slept during the REM-sleep-dominated late half night (Late sleep: group B).

In the delayed recognition task (see Figure 3d), the ANOVA failed to reveal a significant effect of condition or half night, regardless of the type of information, nor did it reveal interaction between these factors (see Table 2).

A significant effect for spatial information only was found for R responses. ANOVA revealed a simple effect of half night ($P < .05$) on R judgments (remember) associated with delayed recognition of spatial information but no effect of condition or interaction between these factors. Subjects placed in the early retention condition, whether sleeping or kept awake, gave significantly more R responses than did subjects placed in the late retention condition. Posthoc analysis indicated that, following REM-sleep deprivation (Late sleep deprivation, group D), subjects gave significantly fewer responses associated with a "Remember" judgment (reflecting episodic memory) than did subjects who were SWS deprived (Early sleep deprivation, group C) ($P < .05$, Cohen's d = 1.24) (see Figure 3e).

DISCUSSION

The present study compared, for the first time, the effects of early and late nocturnal sleep on consolidation of strictly episodic memory, using a task that assessed not only the consolidation of the 3 components of this form of memory, but also the subject's state of consciousness while performing the task. Effects of sleep were also compared with those of wakefulness. Our main result indicates that REM sleep supports the consolidation of spatial episodic information and may also have a beneficial effect on the quality of these memories.

Performance on immediate free recall was not significantly different between early and late retention intervals. The subjects performed equivalently on immediate free recall whenever the learning session occurred. This lack of significant difference between the 4 groups, who learned at different times and under different condition (after prior sleep or wake), argues, at first sight, against substantial effects of fatigue, circadian variation, or sleep inertia. The 15-minute interval after awakening that has been proposed seems to be sufficient to dissipate most of the effects of sleep inertia. This point is underpinned by studies indicating that sleep inertia lasts up to 15 minutes.[32,33] However, other studies have shown that sleep inertia can last at least 30 minutes and is strongest after awak-

ening during SWS (see [34] for review). However that may be, this lack of significant difference between the 4 groups on immediate free recall does not argue against sleep inertia sufficiently affecting memory traces to prevent long-term consolidation.

As for delayed free recall, the effects reported are barely significant but large, as indicated by Cohen's d values. This result must be considered as preliminary and needs replication. Nevertheless, we can suggest that REM-sleep deprivation impairs consolidation of the spatial component of episodic memory. This result is inconsistent with the conclusions of Plihal and Born[35] using a mental spatial rotation task but is, however, consistent with numerous studies in animals indicating a beneficial effect of REM sleep on hippocampal-dependent spatial learning (see [3] for review and [36]). Using nearly the same episodic task we used, Kopelman et al[26] found that patients with temporal lobe lesions, including the hippocampus, were markedly impaired on spatial memory. Moreover, neuroimaging studies have shown that activity in temporal lobe, including the hippocampus, was increased during REM sleep as compared to wakefulness (see [37] for review). This activation could subserve consolidation of spatial information during REM sleep.
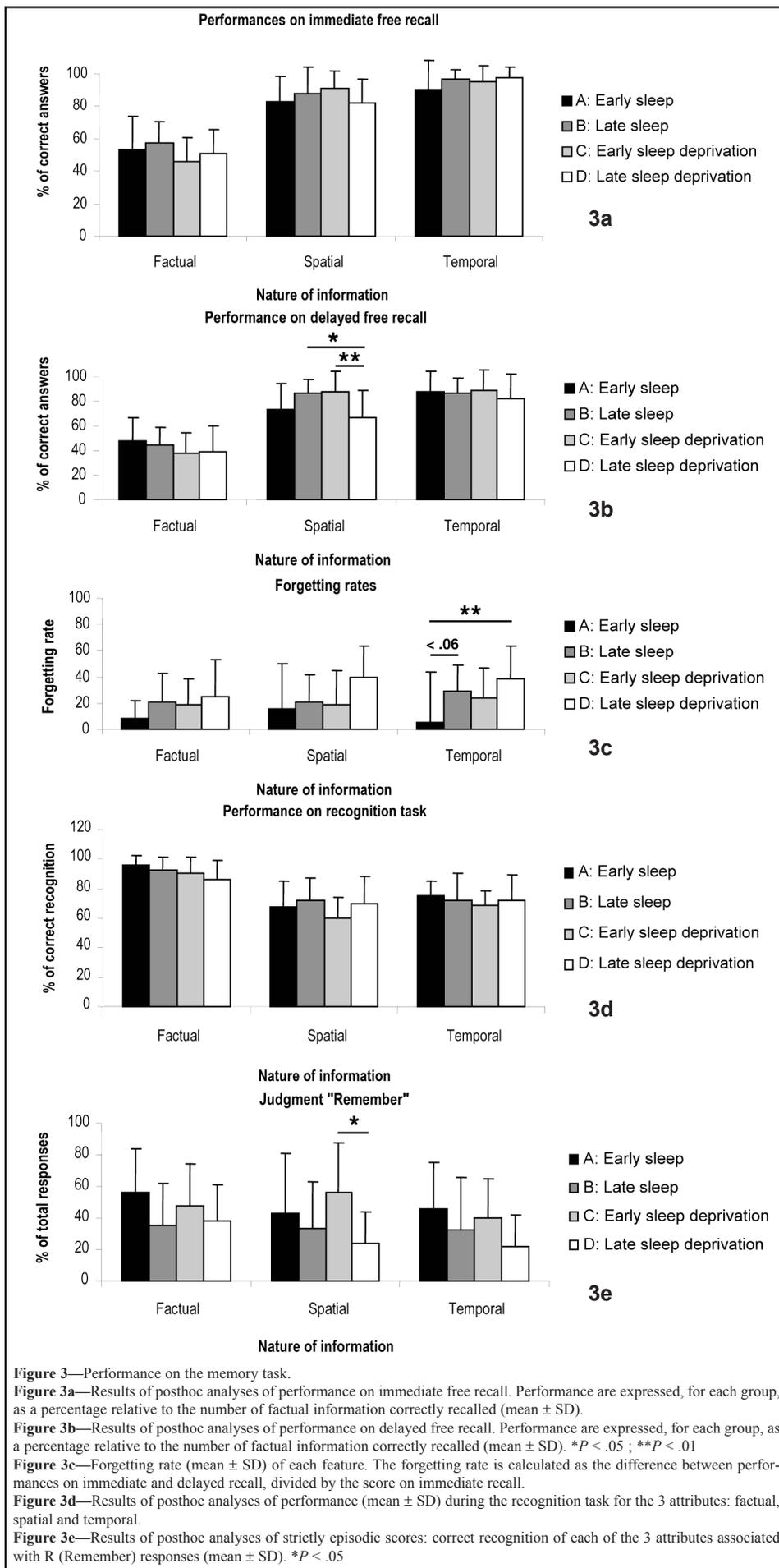
Surprisingly, the performance of REM-sleep-deprived subjects (group D) was not different from that of subjects who slept during the early half night (group A). REM-sleep-deprived subjects learned the 2 lists of words during the least advantageous circadian period, ie, when factors such as attention and vigilance are at their minimum level. In this respect, their performance should have been severely impaired. The lack of significant impairment in these subjects could be due to uncontrollable rehearsal of learned material during the retention interval. Another explanation could be that sleep inertia lasted more than 15 minutes and had affected sufficiently labile memory traces to prevent long-term consolidation. Since the group who had to learn and recall information under sleep-inertia effects (group B: Late sleep) performed better than the group that only learned under sleep-inertia effects (group D: Late sleep deprivation), it appears that sleep inertia may affect learning more than recall. If so, one would expect performance in group D (Late sleep deprivation) to be lower than in group A (Early sleep). Our statistical analyses failed to reveal any significant difference between these 2 groups, suggesting that effects of sleep inertia may have been masked, in part, by a mental rehearsal of learned material during wakefulness.

In regard to temporal information, our results tend to indicate, but do not reach significance, that recall is better after SWS than after REM sleep. This preliminary result, requiring replication, suggests a beneficial effect of SWS on consolidation of the temporal component of episodic memory. We also report a significant increase of the forgetting rate of temporal information in REM-sleep-deprived subjects as compared to subjects in the early sleep condition. Once again, these results could be explained by the fact that sleep inertia especially affects learning. Indeed, subjects in the late sleep condition (group B) or REM-sleep-deprived group (Late sleep deprivation, group D) learned under sleep-inertia effects, whereas subjects in the early sleep condition (group A) did not. Nevertheless, the effects reported are moderate (A vs B) and large (A vs D). Therefore, they seem to be real effects but still need to be confirmed with a paradigm that limits design confounds. Surprisingly, SWS deprivation did not significantly impair delayed recall, suggesting that consolidation could also occur during wakefulness, perhaps due in part to uncontrollable rehearsal of learned

Table 2—Results of the different statistical analyses performed

Score to compare	Analysis of variance Main effect of condition (wake / sleep)	Main effect of half night (early / late)	Interaction	Posthoc tests (Fisher's PLSD)	Effect size (Cohen's d)
Immediate free recall					
Factual	$F_{1,39} = 1.99$; $P < .16$	$F_{1,39} = 0.78$; $P < .94$	$F_{1,39} = 0.00$; $P < .92$	X	X
Spatial	$F_{1,39} = 0.04$; $P < .84$	$F_{1,39} = 0.14$; $P < .7$	$F_{1,39} = 2.61$; $P < .11$	X	X
Temporal	$F_{1,39} = 0.74$; $P < .39$	$F_{1,39} = 1.69$; $P < .2$	$F_{1,39} = 0.39$; $P < .53$	X	X
Delayed free recall					
Factual	$F_{1,39} = 2.02$; $P < .16$	$F_{1,39} = 0.06$; $P < .8$	$F_{1,39} = 0.17$; $P < .68$	X	X
Spatial	$F_{1,39} = 0.24$; $P < .62$	$F_{1,39} = 0.45$; $P < .5$	**$F_{1,39} = 9.11$; $P < .01$**	**B vs D: $P < .05$**	**1.15**
				C vs D: p< 0.001	**1.07**
Temporal	$F_{1,39} = 0.17$; $P < .67$	$F_{1,39} = 0.51$; $P < .47$	$F_{1,39} = 0.21$; $P < .64$	X	X
Forgetting rates					
Factual	$F_{1,39} = 1.10$; $P < .29$	$F_{1,39} = 2.11$; $P < .15$	$F_{1,39} = 0.2$; $P < .65$	X	X
Spatial	$F_{1,39} = 1.73$; $P < .19$	$F_{1,39} = 0.10$; $P < .10$	$F_{1,39} = 0.84$; $P < .36$	X	X
Temporal	$F_{1,39} = 2.86$; $P < .1$	**$F_{1,39} = 5.27$; $P < .05$**	$F_{1,39} = 0.26$; $P < .61$	**A vs B: $P < .06$**	**0.78**
				A vs D: $P < .01$	**1.05**
Delayed recognition					
Factual	$F_{1,39} = 3.09$; $P < .09$	$F_{1,39} = 1.39$; $P < .2$	$F_{1,39} = 0.11$; $P < .73$	X	X
Spatial	$F_{1,39} = 1.02$; $P < .3$	$F_{1,39} = 2.22$; $P < .14$	$F_{1,39} = 0.27$; $P < .6$	X	X
Temporal	$F_{1,39} = 0.54$; $P < .46$	$F_{1,39} = 0.00$; $P < .95$	$F_{1,39} = 0.55$; $P < .46$	X	X
"R" responses					
Factual	$F_{1,39} = 0.13$; $P < .72$	$F_{1,39} = 3.72$; $P < .06$	$F_{1,39} = 0.46$; $P < .49$	X	X
Spatial	$F_{1,39} = 0.04$; $P < .83$	**$F_{1,39} = 5.2$; $P < .05$**	$F_{1,39} = 1.41$; $P < .24$	**C vs D: $P < .05$**	**1.24**
Temporal	$F_{1,39} = 0.96$; $P < .33$	$F_{1,39} = 3.8$; $P < .06$	$F_{1,39} = 0.07$; $P < .78$	X	X

Figure 3—Performance on the memory task.
Figure 3a—Results of posthoc analyses of performance on immediate free recall. Performance are expressed, for each group, as a percentage relative to the number of factual information correctly recalled (mean ± SD).
Figure 3b—Results of posthoc analyses of performance on delayed free recall. Performance are expressed, for each group, as a percentage relative to the number of factual information correctly recalled (mean ± SD). *P < .05 ; **P < .01
Figure 3c—Forgetting rate (mean ± SD) of each feature. The forgetting rate is calculated as the difference between performances on immediate and delayed recall, divided by the score on immediate recall.
Figure 3d—Results of posthoc analyses of performance (mean ± SD) during the recognition task for the 3 attributes: factual, spatial and temporal.
Figure 3e—Results of posthoc analyses of strictly episodic scores: correct recognition of each of the 3 attributes associated with R (Remember) responses (mean ± SD). *P < .05

material. Such rehearsal would have minimized the power to see enhanced memory due to a specific sleep stage. An alternative explanation comes from Plihal and Born's work,[38] which argue in favor of a role of cortisol rather than SWS in memory. Indeed, according to these authors, an infusion of cortisol during SWS impairs the consolidation of episodic memories. In normal conditions, cortisol levels reach a circadian minimum during SWS. Interruption or deprivation of SWS does not prevent the minimum level from occurring. This circadian inhibition of glucocorticoid secretion, during the time when early sleep occurs, could be an essential factor for the consolidation of episodic memories.[39]

The lack of effect of SWS deprivation on consolidation of temporal information is inconsistent with the study of Harrison and Horne,[40] who showed that a 36-hour sleep deprivation affects particularly temporal memory, as assessed by a recency discrimination task. This impairment could, however, be due to other factors such as a reduction of attention capacity or motivation. A possible explanation for the absence of such an effect in our study could be the duration of sleep deprivation (4 hours), which may be insufficient to substantially affect temporal memory. Moreover, subjects deprived of either sleep stage (wake groups) did not forget significantly more temporal information than subjects in the corresponding sleep groups, suggesting that neither stage alone is sufficient to enhance consolidation. Perhaps optimal consolidation of the temporal component of episodic memory requires successive processing in both sleep stages. In that sense, further investigations seem necessary.

Performance on delayed recognition were not significantly different across any group. This task, consisting of forced choice recognition between 2 items, thus seems less sensitive to the effects of sleep deprivation than is the delayed free recall task.

Concerning scores of autonoetic consciousness, statistical analyses revealed that SWS-deprived subjects gave significantly more R responses, indicative of truly episodic memories, than did REM-sleep-deprived subjects. This result cannot be explained only by circadian variations in factors such as attention, fatigue, or alertness. Indeed, such an influence would have been expected to result in a comparable pattern of changes whether subjects were asleep or awake. Remembering the spatial localization of an item (ie, the location of the words on a page) may involve the same cognitive process as a visual-discrimination task. We suggest that the more accurate this discrimination, the more detailed the spatial memories. In this way, a marked reduction of R responses after REM-sleep deprivation is in agreement with the finding that REM sleep has a beneficial effect on performance on a visual discrimination task.[9] Thus REM-sleep deprivation impairs not only the extent of episodic memory as assessed by delayed recall of spatial infor-

mation, but also the vividness of this memory.

Prospects

The effect of SWS on consolidation of temporal information must be considered as preliminary and requiring replication. In order to conclude in favor of a beneficial effect of one sleep stage or another on temporal memory, it would be useful to further investigate this memory component using methodologies that allow more precise assessment of the temporal aspect of memory. For example, subjects could be required to memorize information in more radically different temporal contexts. Computerized tasks, based upon techniques of virtual reality, would also be useful for subjects to learn information in different spatial contexts. Moreover, in order to better control for sleep-inertia effects, an interval lasting at least 30 minutes should be proposed between waking and testing, and subjects should be woken up during light sleep.

In summary, the effects noted in this study are overall modest; sleep deprivation and sleep itself do not have significant effects on numerous variables examined, except on the delayed free recall task, which seems to be more sensitive to sleep deprivation than the other tasks used. Nevertheless, our results indicate that consolidation of the spatial component of episodic memory involves REM sleep. Our data also suggest that REM-sleep deprivation impairs the episodic quality of spatial memories, assessed with a R/K paradigm. Further investigations are necessary to confirm the trend observed in this study toward a possible beneficial effect of SWS on consolidation of the temporal component of episodic memory. If this result is confirmed, these data would be in agreement with the sequential hypothesis proposed by Giuditta et al[15] and supported by several studies of implicit memory consolidation,[13,14] implicating both SWS and REM sleep in memory consolidation.

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