Sleep enhances explicit recollection in recognition memory

Spyridon Drosopoulos,[1] Ullrich Wagner, and Jan Born

University of Lübeck, Department of Neuroendocrinology, D-23538 Lübeck, Germany

Recognition memory is considered to be supported by two different memory processes, i.e., the explicit recollection of information about a previous event and an implicit process of recognition based on an acontextual sense of familiarity. Both types of memory supposedly rely on distinct memory systems. Sleep is known to enhance the consolidation of memories, with the different sleep stages affecting different types of memory. In the present study, we used the process-dissociation procedure to compare the effects of sleep on estimates of explicit (recollection) and implicit (familiarity) memory formation on a word-list discrimination task. Subjects studied two lists of words before a 3-h retention interval of sleep or wakefulness, and recognition was tested afterward. The retention intervals were positioned either in the early night when sleep is dominated by slow-wave sleep (SWS), or in the late night, when sleep is dominated by REM sleep. Sleep enhanced explicit recognition memory, as compared with wakefulness ($P < 0.05$), whereas familiarity was not affected by sleep. Moreover, explicit recognition was particularly enhanced after sleep in the early-night retention interval, and especially when the words were presented with the same contextual features as during learning, i.e., in the same font ($P < 0.05$). The data indicate that in a task that allows separating the contribution of explicit and implicit memory, sleep particularly supports explicit memory formation. The mechanism of this effect appears to be linked to SWS.

Recognition memory refers to a basic form of memory retrieval that has been widely used in experimental psychology. It is assumed that recognition performance is based on two different processes (Yonelinas 2002; Rugg and Yonelinas 2003). One refers to a conscious or explicit process of recollection, where the person initially searches for qualitative information about the context in which the event to be remembered took place. The other process refers to the experience of familiarity, induced automatically or implicitly at a reoccurrence of an event, and can emerge in the absence of any conscious knowledge about the context in which the event originally occurred. The two forms of memory involved in recognition can be separated and show different sensitivity to experimental manipulations. For example, elaborated encoding of stimuli and their context facilitates explicit recollection, but leaves judgments of familiarity at later recognition tasks rather unaffected (Yonelinas 2002). Explicit recollection and familiarity-based implicit processes of recognition are probably supported by distinct neuronal systems. Studies in brain-lesioned patients indicate that the hippocampus is critical for conscious recollection, whereas this seems not to be the case for familiarity-based judgments (Manns and Squire 2001; Yonelinas et al. 2002). Correspondingly, studies using functional magnetic-resonance imaging have shown that the hippocampus is more active when recognition is based on recollection rather than on familiarity (Cansino et al. 2002; Dobbins et al. 2003). Here, we were interested in whether these two forms of recognition memory are differentially affected by sleep.

Sleep is considered to be a brain state, optimizing the consolidation of memories (Maquet 2001; Stickgold et al. 2001). Further, the consolidation of different types of memory seems to be tied to different sleep stages (Born and Gais 2003). In humans, sleep in the early part of the night, dominated by extensive epochs of slow wave sleep (SWS), has been found to enhance, in particular, declarative memories, which refer to episodic and se-

mantic memory and essentially rely on the hippocampal formation (Fowler et al. 1973; Plihal and Born 1997, 1999). This effect has been related to a higher proportion of SWS as compared with rapid eye movement (REM) sleep during early sleep, as well as to accompanying low levels of cholinergic activity in the hippocampus (Hasselmo 1999; Gais and Born 2004). On the other hand, for nondeclarative forms of memory, such as priming, which is considered an implicit form of memory and procedural memory that refers to sensory motor skills, and among others, strongly relies on cortico-striatal circuitry, a greater benefit has been found after periods of late nocturnal sleep (Plihal and Born 1997, 1999; Wagner et al. 2003). This late period of nocturnal sleep is characterized by high amounts of REM sleep, and contains little SWS. While not independent of SWS, procedural memory thus appears to be particularly strengthened by REM sleep-related mechanisms (Gais et al. 2000; Stickgold et al. 2000; Fischer et al. 2002).

So far, most of the studies examining the effects of sleep on memory consolidation in different memory systems used different tasks for this comparison. During the acquisition of task stimuli, both explicit and implicit memories are developed in parallel (Tulving et al. 1999; Willingham and Goedert-Eschmann 1999). In order to separate these two forms of memory at later retrieval testing, a number of recognition tasks have been developed that offer the opportunity to access the two memory systems in the framework of the same task. The process-dissociation procedure by Jacoby (1991) is one such approach that separates explicit recollection from implicit familiarity-based use of memory during recognition. The procedure provides a mathematical approach for the calculation of estimates of explicit and implicit memory in recognition tasks. The contribution of explicit recollection to recognition is estimated primarily on the basis of the subject's responses, indicating that he/she correctly identifies where and when a previously encountered stimulus occurred (e.g., a word is correctly classified as belonging to a certain study list). The use of familiarity-based implicit memory is estimated as the conditional probability of correctly recognizing an item as one that has been previously seen, given it was not recollected (see Methods for a detailed description). Both esti-

[1]**Corresponding author.**
E-mail drosopoulos@kfg.mu-luebeck.de; fax 49-51-5003640.

mates of recollection and familiarity-based memory have been found to vary statistically independently under different experimental conditions (Yonelinas 2002).

The purpose of the current study was to compare influences of early SWS-rich periods of retention sleep with late REM sleep-rich periods of retention sleep on estimates of explicit and implicit memory in a word-recognition paradigm, using the process-dissociation procedure. Based on previous studies showing that declarative memory (hippocampus-dependent) improves, in particular from SWS, we expected explicit recollection (also hippocampus-dependent) to benefit primarily from SWS as well. Moreover, explicit hippocampus-dependent memory was expected to benefit, particularly when recollection is based on a more elaborate use of contextual features (i.e., when a word at recognition testing is presented in the same font as at acquisition, as compared with a presentation in a different font). On the other hand, familiarity-based implicit recognition, being a nondeclarative type of memory, was expected to benefit, in particular, from REM-sleep rich periods of sleep. Participants had to learn two lists of words and they also had to memorize which list each word belonged to. The words were presented in two different fonts, which changed in half of the words at recognition testing (contextual congruency manipulation). Learning was followed by a 3-h retention interval filled with either SWS-rich sleep or REM-rich sleep, and recognition was tested 15 min after sleep. In a control group, the 3-h retention intervals were spent awake. Saliva cortisol, measured to control for possible confounding effects of glucocorticoid release on memory, was sampled before and after the retention intervals.

Results

Sleep and cortisol

Table 1 summarizes polysomnographic results for the early and late-night retention intervals and associated concentrations of cortisol. Total sleep time, as well as the percentages of wakefulness, stage 1 sleep (S1), and stage 2 sleep (S2), did not differ significantly from each other [$F_{(1,20)}$ = 0.14, 2.52, 2.51, 1.44, respectively, $P > 0.13$]. Percentages of SWS and REM sleep exhibited the typical and highly robust differences, with the percentage of SWS being almost four times higher in the early than late-night retention sleep, whereas the percentage of REM sleep was almost three times higher in the late-night retention sleep [$F_{(1,20)}$ = 88.6, $P < 0.001$, and $F_{(1,20)}$ = 45.69, $P < 0.001$, respectively]. Sleep prior to learning in the late night (not included in Table 1) did not

Table 1. Sleep and cortisol data

Parameter	Early night		Late night		
	Mean	SEM	Mean	SEM	P<
Sleep time (min)	195.75	4.89	193.00	5.36	n.s.
Wake (%)	2.13	0.61	3.56	0.67	n.s.
S1 (%)	4.13	0.88	6.21	0.97	n.s.
S2 (%)	48.90	2.08	52.62	2.28	n.s.
SWS (%)	34.81	1.69	9.25	1.86	<.001
REM (%)	9.12	1.67	28.37	1.83	<.001
Sleep cortisol (µg/dl)	0.11	0.03	0.23	0.05	<.001
Wake cortisol (µg/dl)	0.08	0.03	0.36	0.06	<.001

(S1) Stage 1 sleep; (S2) stage 2 sleep; (SWS) slow wave sleep; (REM) rapid eye movement sleep. Cortisol values for the sleep and wake group for early and late-night retention interval, estimated by average concentration in samples collected immediately before and after the retention interval. (Right column) Results from pairwise comparisons between the effects of early and late night. (n.s.) Not significant.

differ between the sleep and the wake group. The respective values for the sleep and wake group were as follows: total sleep time, 196.21 ± 5.49 versus 195.91 ± 5.73 min; S1, 6.96 ± 1.82 versus 6.30 ± 1.91%; S2, 41.81 ± 2.96 versus 45.28 ± 3.09%; SWS, 37.78 ± 4.19 versus 34.59 ± 4.38%; REM sleep, 10.18 ± 1.90 versus 10.67 ± 1.98%, ($P > 0.15$, for all comparisons).

As expected, saliva cortisol values indicated significantly lower cortisol concentrations during the early than during late-night retention intervals [$F_{(1,21)}$ = 23.07, $P < 0.001$] (Table 1), but the levels did not differ between the sleep and wake groups, [$P > 0.12$, for all comparisons].

Recognition performance

Immediate recognition testing on a number of recognition tasks at learning, introduced as a control for performance differences during the learning phase, revealed an overall low performance, which, however, was clearly better than chance ($P < 0.01$). There were no significant differences between the early and late-night conditions, as well as between the sleep and wake groups in this control task. Explicit recollection scores at this task were 0.22 ± 0.07 for the early sleep condition, 0.24 ± 0.07 for the early wake condition, 0.24 ± 0.06 for the late sleep condition, and 0.19 ± 0.06 for the late wake condition ($P > 0.60$ for all comparisons). The respective values for familiarity-based judgements were 0.33 ± 0.04, 0.32 ± 0.05, 0.37 ± 0.03, and 0.35 ± 0.03 ($P > 0.34$ for all comparisons).

Recognition testing after the retention interval on the word lists revealed distinct differences, depending on the type of memory as well as on the type of retention interval (Table 2A). Explicit recollection was generally enhanced after retention intervals of sleep in comparison to wake intervals [main effect for sleep/wake manipulation, $F_{(1,22)}$ = 4.33, $P < 0.05$]. The enhancing effect of sleep on explicit memory was particularly pronounced after early-night retention sleep and especially for the context congruent words (Fig. 1A), as revealed by the significant three-way "sleep/wake" × "night-half" × "context congruency" interaction [$F_{(1,22)}$ = 4.29, $P = 0.05$]. No other effect approached significance [$F_{(1,22)} < 2.74$, $P > 0.12$, for all comparisons]. The pattern of the three-way interaction was also confirmed in a post-hoc analysis. First, one-way ANOVAs showed that the sleep and wake group differed primarily in recollection of congruent words in the early night [$F_{(1,11)}$ = 7.50, $P < 0.05$]. In the late night, this effect failed to reach the 5% level of significance [$F_{(1,11)}$ = 3.18, $P < 0.10$]. Additionally, for the incongruent words, the difference between the sleep and wake group did not approach significance either in the early-retention interval [$F_{(1,11)}$ = 0.95, $P > 0.34$] or in the late-night retention interval [$F_{(1,11)}$ = 2.80, $P > 0.11$]. Furthermore, two-way ANOVAs performed separately for the sleep and wake group showed a significant effect for the "night-half" × "context congruency" interaction [$F_{(1,11)}$ = 5.09, $P < 0.05$] in the sleep group. The direction of this effect was further investigated by paired t-tests, which confirmed the enhanced explicit recollection of words presented in congruent context in the early-night retention sleep over both (1) the same words in the late-night retention sleep ($P < 0.05$), and (2) the words presented in incongruent context in the early-night retention sleep ($P < 0.05$, Fig. 1A). The difference between words presented in congruent and incongruent context in the late-night retention sleep, or between the incongruent words in the early and late-night retention sleep, did not approach significance ($P > 0.59$ for both comparisons). The analyses in the wake group showed no significant effects [$F_{(1,11)} < 0.54$, $P > 0.48$ for all comparisons].

For the familiarity-based recognition scores, congruent words were slightly better remembered than the incongruent words [$F_{(1,22)}$ = 3.10, $P < 0.10$] (Table 2; Fig. 1B). However, there

Table 2. Recognition performance after early and late night retention intervals.

A. Early night retention interval

		Congruent words			Incongruent words		
		True pos	False pos	Know	True pos	False pos	Know
Responses	Sleep	0.71	0.10	0.04	0.64	0.12	0.03
	Wake	0.59	0.21	0.05	0.58	0.16	0.06
Recollection	Sleep		0.60 ± 0.06			0.52 ± 0.07	
	Wake		0.37 ± 0.06			0.41 ± 0.07	
Familiarity	Sleep		0.37 ± 0.03			0.32 ± 0.03	
	Wake		0.41 ± 0.03			0.36 ± 0.03	

B. Late night rentention interval

		Congruent words			Incongruent words		
		True pos	False pos	Know	True pos	False pos	Know
Responses	Sleep	0.62	0.15	0.04	0.61	0.12	0.06
	Wake	0.51	0.16	0.07	0.51	0.14	0.08
Recollection	Sleep		0.47 ± 0.05			0.49 ± 0.05	
	Wake		0.35 ± 0.05			0.36 ± 0.05	
Familiarity	Sleep		0.36 ± 0.03			0.35 ± 0.04	
	Wake		0.34 ± 0.03			0.34 ± 0.04	

Mean ± SEM scores of explicit recollection and familiarity-based implicit memory in the early and late night retention interval. Respective upper lines indicate mean proportions of actual button press responses of true positive (correctly identified old words with correct list classification), false positives (correctly identified old words with wrong list classification), and "know" classifications (correctly recognized old words but without list membership classification, i.e., true positives button "4").

was no general effect of sleep on familiarity-based recognition scores [$F_{(1,22)} = 0.13$, $P > 0.70$], and these scores also did not differ between early and late-night retention intervals [$F_{(1,22)} > 2.07$, $P > 0.17$].

A supplemental control analysis showed no effect of the "sleep/wake" or the "night-half" manipulation on the ability to identify the new words. The percentages for correctly identified new words were well above chance and did not differ from each other (sleep group in the early night 78.68 ± 5.48%, in the late night 78.20 ± 5.30%, wake group in the early night 75.66 ± 5.48%, in the late night 77.47 ± 5.30%, $F_{(1,22)} < 0.13$, $P > 0.70$ for all comparisons). Moreover, control analyses did not indicate any significant correlations between scores of recollection and familiarity ($P > 0.14$). The respective coefficients were in the sleep group r = 0.06 (early retention interval—congruent words), r = −0.17 (early retention interval—incongruent words), r = −0.10 (late retention interval—congruent words), and r = 0.01 (late retention interval—incongruent words). In the wake group, the respective coefficients were r = −0.38, −0.38, −0.40, and −0.46, respectively.

Questionnaires

After having completed the word-recognition task at retrieval, subjects rated their current feelings of activation, drowsiness, tiredness, motivation, and concentration. In general, all variables, including tiredness (early sleep, 3.58 ± 0.28 vs. early wake, 3.92 ± 0.28, late sleep, 3.50 ± 0.28 vs. late wake, 4.00 ± 0.28) and subjective concentration (early sleep, 2.83 ± 0.27 vs. early wake, 2.42 ± 0.27, late sleep, 2.75 ± 0.27 vs. late wake, 2.67 ± 0.27), were closely comparable for both groups for both night intervals at retrieval testing ($P > 0.13$, for all comparisons). None of the participants had noticed the change in fonts in the recognition task, although some (two in the sleep group and one in the wake group) said that they thought something was "strange" with some words.

Control experiments on retrieval function

In light of evidence that performance on tasks relying on the frontal cortex are highly sensitive to an impairing influence of sleep deprivation (Harrison and Horne 1998; Drummond et al. 2000), and since explicit recollection also involves this brain region (Fletcher and Henson 2001), additional experiments in two separate groups of subjects ($n = 22$, age 20–35 yr) examined whether a 3-h period of early wakefulness induced any sleep deficit that would account for the inferior explicit recollection seen in this condition in the main study. A phonetic fluency task used to assess fluency of word retrieval from long-term memory (Aschenbrenner et al. 2000; a German adaptation of a test originally developed by Christensen and Guilford [1958]) required the subject to write down as many words as possible within 2 min, starting with a certain letter ("p", "m"). The task was presented before and after 3-h periods of sleep ($n = 12$) and wakefulness ($n = 10$) during the early night, scheduled in the same way as in the main experiments. Also, the digit-span test (forward and backward) was presented to assess general prefrontal-mediated working memory function. Retrieval fluency after the 3-h periods did not differ between the sleep and wake groups [$F_{(1,20)} < 1.40$, $P > 0.25$ for all comparisons], and was, on average, even slightly higher in the wake group (Table 3). Also, digit-span test performance was closely comparable between the groups [$F_{(1,20)} < 1.60$, $P > 0.22$ for relevant comparisons] and [$F_{(1,20)} < 2.18$, $P > 0.16$ for all comparisons] for both forward and backward, respectively (Table 3).

Discussion

This study used the process-dissociation procedure (Jacoby 1991) to separate effects of sleep on explicit and implicit memory consolidation. Compared with retention periods of wakefulness, sleep generally enhanced measures of explicit recollection. This effect was particularly pronounced during early sleep periods dominated by SWS, and when, at recognition testing, the words were presented in the same font, as at learning before sleep. In-

Table 3. Effects of early sleep and wakefulness on retrieval function and working memory

	Fluency of word retrieval		Digit span (forward)		Digit span (backward)	
	Before	After 3 h	Before	After 3 h	Before	After 3 h
Sleep	20.17 ± 1.54	19.83 ± 1.57	9.08 ± 0.70	9.92 ± 0.58	7.58 ± 0.48	8.25 ± 0.55
Wake	19.70 ± 1.68	22.60 ± 1.72	8.30 ± 0.77	8.50 ± 0.63	7.80 ± 0.52	7.50 ± 0.60

Mean ± SEM scores for fluency of word retrieval and digit-span test performance (forward and backward).

terestingly, familiarity-based implicit memory did not benefit from sleep. There, only a small benefit was observed for contextual congruency (i.e., when the font of the words was kept the same at retrieval as at learning), which, however, was independent of sleep. As a whole, these results speak for a greater sensitivity of explicit than implicit memory formation to the enhancing effects of sleep that might be particularly linked to SWS.

The effects of sleep observed cannot be attributed to circadian variations, since changes in memory across periods of early and late sleep were compared with periods of wakefulness in the same phase of the circadian rhythm. This is also supported by the fact that saliva cortisol concentrations were closely comparable between the sleep and wake conditions, and at the same time, showed the normal circadian variation. Likewise, self ratings of fatigue and concentration did not differ between the groups at learning and retrieval testing. In addition, although at an overall low-performance level, immediate recognition (of numbers) tested at learning did not differ either between sleep and wake groups or within each of these groups when tested in the evening or at night.

The results of our control experiment also argue against the view that the wake periods of about 3 h during the early night induced any substantial effects arising from sleep deprivation. This experiment was conducted on the background of evidence that sleep deprivation (for 36 h) has an impairing influence, particularly on prefrontal-mediated retrieval functions (Harrison and Horne 1998; Drummond et al. 2000). Our results show that word retrieval from long-term memory, as well as working-memory functions, remained unaffected by a 3-h sleep deprivation in the early night as compared with early sleep. With regard to our finding of enhanced explicit recollection of context congruent words after early retention sleep, it should be emphasized that this effect was not only significant in comparison with early wakefulness, but also in comparison with late retention sleep (Fig. 1).

A benefit of the process-dissociation procedure is that within the same task, the effects of sleep on explicit and implicit memory can be assessed simultaneously. This is important, since earlier studies indicating a differential sensitivity to the effect of sleep and sleep stages depending on the type of memory system relied mostly on completely different tasks to assess the respective memory systems. Using the same task to test explicit and implicit memory rules out that the differential effects of sleep observed here were due to some nonspecific task characteristics not related to any of the two memory systems.

Our finding of a distinctly more pronounced improvement of explicit recollection after retention periods of early rather than late-night sleep agree with a number of previous studies, indicating a particular benefit of hippocampus-dependent declarative memory from just this early period of SWS-rich sleep (Born and Gais 2003). It has been proposed that the enhancing effect of early sleep on hippocampus-dependent memories relies on a reactivation of the newly acquired memory representations in hippocampal neuronal populations that occurs predominantly during SWS (Hasselmo and Wyble 1997; Buzsáki 1998; McNaughton

et al. 2003). Such processes could explain a facilitated access at later explicit recollection of these memories. An involvement of the hippocampal formation in the sleep-associated memory process of interest is further supported by our finding that explicit memory enhancement during early sleep was most robust when the words were presented in the same context as during encoding. Several previous studies have consistently shown that one essential hippocampal function serves to bind encoded information with contextual cues, even in the absence of awareness for these contextual cues (Henke et al. 1999, 2003; Stark and Squire 2001). Thus, a contextual dependence of the explicit memory enhancement during early sleep seems to be in agreement with the notion that this type of sleep particularly benefits hippocampus-dependent types of memory.

Contrary to our expectation, familiarity-based measurements of implicit memory were not enhanced by sleep, either during the early part or during the late part of the night. While this negative finding agrees with a recent study testing effects of early and late sleep on performance in a "remember/know" paradigm (Rauchs et al. 2004), it appears to contrast with a number of foregoing studies indicating that various forms of nondeclarative memory, such as the procedural memory for skills (Plihal and Born 1997) and the priming of words and faces (Plihal and Born 1999; Wagner et al. 2003) benefit in particular from REM sleep-rich periods of sleep. Those studies led us to suppose a generalized benefit for REM sleep-rich periods of sleep for nondeclarative memories not depending on hippocampal function. However, it is not unlikely that familiarity, priming and procedural tasks, apart from relying on nonhippocampal brain regions, actually represent different types of memory (Wagner et al. 1998; Drummond et al. 2000, Stark and Squire 2000; Rugg and Yonelinas 2003), and thus, may differ in other qualities that are crucial to their sensitivity to the enhancing effect of sleep.

In addition, there are hints that memory based on familiarity judgments decreases at a more rapid rate than recollection based memories (Yonelinas and Levy 2002). It could be that in our experiment, the time spent between encoding and retrieval was too long for any difference in familiarity-based judgments to remain detectable. However, this possibility seems unlikely according to the background of evidence that when relatively long time intervals in the order of hours (and even days) are tested as in the present study, decline rates of familiarity were found not to be greater than those for measures of recollection (Hockley and Consoli 1999).

The absence of effects of retention sleep on familiarity-based recognition could have its origin also in more general conceptual implications of the process-dissociation procedure that has not remained without criticism (Richardson-Klavehn et al. 2002; Mintzer et al. 2003). In particular, it is still under debate whether recollection and familiarity indeed are linked to two different memory systems, or whether they refer to different retrieval mechanisms at recall to gain access to the same memory trace (Ratcliff et al. 1995). Along this line of reasoning, the failure to find effects on familiarity-based implicit recognition scores here may just reflect a less-efficient access to the memory trace of
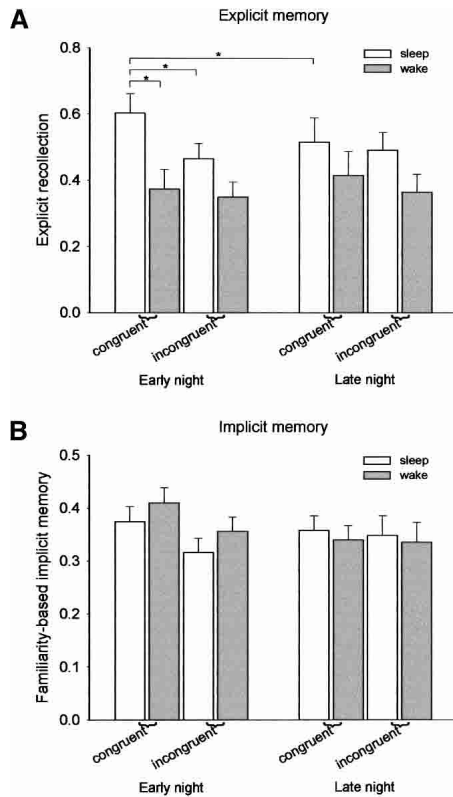
Figure 1. Mean ± SEM scores for (*A*) explicit recollection and (*B*) familiarity-based implicit memory, as derived from the process-dissociation procedure for the sleep (white bars) and the wake group (gray bars) after early and late-night retention intervals separately for words presented in the same font as during acquisition (congruent context) as well as for words presented in a changed font (incongruent context). Note, sleep generally enhanced explicit recollection, and especially for the congruent words after early sleep. There were no significant effects of sleep on familiarity-based implicit memory scores. (*) $P < 0.05$ for pairwise comparisons.

interest via this type of recognition judgement. Related to this, from the perspective of the process-dissociation procedure, the contextual effect that we observed in our study on explicit memory was also not expected. This is because manipulations of the perceptual features of stimuli in general are considered to affect only implicit forms of memory such as priming (Fleischman et al. 1997). Diverging from this view, our findings suggest that nonconsciously attended information influenced explicit memory. This raises the problem of contamination, i.e., the possibility of partial overlaps between explicit and implicit memory (Butler and Berry 2001), and thus implies a violation of the independence assumption of the process-dissociation procedure, which regards explicit recollection and familiarity-based implicit recognition as entirely independent from each other. Accordingly, the pattern of our results brings into question the notion that measures of implicit and explicit memory reflect memory systems as different and independent, as assumed by the process-dissociation procedure, although (post-hoc) linear correlation analyses of our data assured that scores of recollection and familiarity-based judgments were independent in a statistical sense. Adopting a perspective beyond the framework of the process-dissociation procedure, the present data would indicate that recognition of old words remains uninfluenced by sleep, but that after early sleep, the subject's ability to identify the correct list for congruent words is enhanced. This view appears to be in line with findings from a recent study that early SWS-rich sleep en-

hances memory for temporal context information in an episodic memory task (Rauchs et al. 2004).

Our data of a selective enhancement of signs of explicit recollection by retention sleep are in line with previous reports of a preferential enhancement of explicitly guided memory during sleep (Robertson et al. 2004). Those studies were based on serial reaction time tasks (SRTT), and showed that offline improvement in task performance that occurred selectively across retention periods of sleep required that subjects were aware of the sequence of the task they trained for before sleep. Recent experiments indicated that the hippocampus and closely connected temporal lobe structures can be involved in both explicit and implicit learning on the SRTT (Schendan et al. 2003). Thus, activation of prefrontal cortical circuitry, including the dorsolateral and ventrolateral prefrontal cortex, seems to be more relevant to the distinction between explicit and implicit processes on that task (Fletcher and Henson 2001; McIntosh et al. 2003), which may apply to the recognition task used here as well. Notably, some evidence exists that slow oscillatory EEG activity dominating human SWS reflects processes of cortical reorganization, especially in the prefrontal cortex, that could be linked to explicit processing (such as thinking) taking place during the wake phase (Anderson and Horne 2003a,b; Steriade and Timofeev 2003). From this perspective, use-dependent changes in prefrontal cortical circuitry during explicit processing in the wake phase could be a starting point for plastic changes underlying memory formation during SWS-rich sleep (Sejnowski and Destexhe 2000; Huber et al. 2004; Mölle et al. 2004).

Methods

Participants

Twenty-four healthy, nonsmoking, drug-free subjects with no prior history of sleep disturbances participated in the main experiments and received a money reward for their participation (12 males; mean age 23.0 yr, range 19–28 yr). Subjects orally reported to habitually sleep 7–9 h per night, and not to have had any major disruption of the sleep-wake cycle during the 6 wk before experimentation. Subjects were acclimated to the experimental sleep condition by spending an adaptation night in the sleep laboratory, including the placement of electrodes. On the two experimental days, the participants were instructed to get up at 7:00 h and not to take any naps during the day. They were instructed not to ingest alcohol or (after 15.00 h) caffeine containing drinks on these days. The study was approved by the local ethics committee. All participants gave written informed consent before participation.

Design and procedure

The experiment included two groups, a sleep group and a wake control group (six men and six women in each group). Each group was examined in an early and a late-night retention interval, with the order of the conditions balanced across subjects. The two experimental nights were separated by an interval of at least 1 wk. In the early retention condition, participants reported to the laboratory at 21:30 h. After electrodes were applied for standard polysomnography (only in the sleep group), participants performed in the recognition task from 22:15–23:00 h (learning phase). In the sleep group, the participants went to bed afterward. Three hours after sleep onset, participants were awakened as soon as S1 or S2 sleep occurred. Awakening from SWS or REM sleep was avoided, as this can decrease subsequent retrieval performance (Stones 1977). Fifteen minutes after awakening, retrieval in the recognition task was tested. The participants in the wake group remained awake during the 3-h retention interval between initial learning and retrieval testing. During this time, they watched movies, played (computer) games, or engaged in conversations with the experimenter.

In the late retention condition, participants came to the lab at 22:30 h. After electrodes for sleep recordings were applied, subjects went to bed and were awakened 3 h after sleep onset, as soon as sleep S1 or S2 occurred. Fifteen minutes later, the learning phase took place (2:15–3:00 h). Thereafter, participants in the sleep group went back to bed and slept for another 3 h. Again, 15 min after awakening, retrieval was tested (6:15–7:00 h). As in the early retention condition, the participants in the wake group stayed awake for 3 h after learning.

After having performed the recognition task, participants rated their current feelings of activation, drowsiness, tiredness, motivation, and concentration on five-point rating scales. Saliva cortisol was sampled before and after the retention intervals. (Results from additional samples taken before and after testing did not add any relevant information, and hence, are not reported here). At the end of the entire experiment, the participants were asked whether they had noticed the change in fonts that had taken place in some words during the recognition task.

Task materials

The words of the recognition task were selected from the Toronto word pool and translated to German. Of the 306 words selected, 18 words were used as buffer words, the remaining 288 were divided into six lists (each 48 words) balanced for imagery, frequency, and concreteness. Three lists were used for each retention interval. Two served as study lists and one served as a novel one, the words of which were presented only during recognition. The words were presented using WespXP 1.98 (freeware from the Department of Psychology at the University of Amsterdam) on a 17-inch monitor, screen area was 1024 by 864 pixels using the 16-bit color mode, refresh rate was set on 75 Hz. Two true-type (.ttf) windows-compatible fonts (font size 48) able to express special characters were used to present the words (i.e., "tsp tonight 1.ttf" and "tsp mcis 2.ttf").

Recognition task

Two lists of words were presented at learning, each starting with three buffer words, followed by 48 study words. All words were presented randomly, one at a time, on a computer screen in front of the subject. The words were presented in white on a black background for 4.5 sec with an interval of 1 sec between each word. Half of the words were presented in one font and the other half in the other. The subjects were instructed to memorize the words and also to memorize which of the two lists each word belonged to. They were told that some words would be harder to read than others (although this was not the case) by presenting them in different fonts.

During recognition testing after the retention interval, a list of words was presented that started with nine buffer words (three from each study list plus three new ones), followed by 144 test words. These test words included, in random order, all words from the two study lists and, in addition, 48 new words. Half of the words from each study list were presented in their original font ("congruent" word presentation), while the other half of the words were presented in the other font, i.e., changed from "tsp mcis 2" to "tsp tonight 1" and vice versa ("incongruent" words). Subjects were asked to respond to each word with their right hand by pressing one of four buttons on a box within 3.5 sec. They were instructed to press button 1 or button 2 (from left to right) if they remembered that the word belonged to either the first or the second list, respectively. Button 3 was to be pressed when the word was new to them and button 4 when the subject knew he/she had seen the word during acquisition, but could not remember which list it belonged to. The 3.5-sec response interval gave the subject ample time for the decisions, which is also supported by the fact that the recollection scores obtained here overall resembled those obtained under conditions of unlimited response time in previous studies (Yonelinas and Jacoby 1996).

To control for possible differences in encoding levels during the learning phase, the presentation of the study word list was preceded by a similar recognition task using three-digit numbers as stimuli instead of words and, most important, with recognition tested immediately after acquisition. Here, each list consisted of only eight numbers with one buffer number. In the recognition test, one buffer number and eight new numbers were added, and the font did not change in this task.

Data analysis

Estimates of recollection and familiarity were derived from scores of inclusion and exclusion, according to the process-dissociation procedure as has been described for the word-list discrimination task (Yonelinas and Jacoby 1996). The inclusion score defines the amount of old words for which the subject correctly remembered the list they belonged to (buttons 1 and 2) plus the old words, which the subject knew he/she had seen during acquisition, but did not remember their list membership any more (button 4). This results in: inclusion = (true positive list1) + (true positive list2) + (true positive button 4). Exclusion is defined as the amount of old words that were falsely remembered to belong to a certain list, i.e., the words from list 1 that were classified under list 2 and vice versa (buttons 1 and 2 again), plus again the old words, of which the subject knew he/she had seen during acquisition, but did not remember their list membership any more (button 4), resulting, respectively, in: exclusion = (false positive list1) + (false positive list2) + (true positive button 4). Inclusion and exclusion scores are then filled in the known formulas for recollection and familiarity as provided by Jacoby's process-dissociation procedure being "recollection = inclusion − exclusion" and "familiarity = exclusion/(1 − recollection)", respectively (Yonelinas and Jacoby 1996). False alarms, delayed responses (>3.5 sec), and buffer words were not included in the calculations.

The procedure used here differs from the original process-dissociation procedure used by Yonelinas and Jacoby (1996), in that it was based on four, rather than two different button press responses, requiring a slightly different behavioral strategy. However, the principles of the process dissociation in our procedure remained the same as in the original procedure. In the original procedure, each of the two buttons are used to indicate a combination of two different decisions. Thus, one is used to indicate that a word is remembered to belong to one of the lists, and additionally, to indicate that a word is "known" when the list membership cannot be remembered. The other button is likewise used to indicate that a word is remembered to belong to the respective other list and additionally to indicate whether a word is "new". Because we wanted to avoid this complex double mapping of response decisions, participants had four buttons in our study, one for every type of response (i.e., two buttons to indicate a word's list membership, and two for "know" and "new" responses, respectively). The calculation of the estimates for explicit recollection and implicit familiarity are not affected by this change, with the inclusion score as in the original procedure reflected by the sum of old words correctly remembered, plus the correct "know" responses and the exclusion score reflected by the sum of false decisions regarding list membership, plus the correct "know" decisions.

Statistical analysis was performed on the scores of recollection and familiarity-based recognition using analysis of variance (ANOVA) including a between subject factor "sleep/wake" and two repeated measures factors "night-half" (early vs. late-night retention interval) and "context congruency" (congruent vs. incongruent font). Post-hoc product moment correlations were calculated between recollection scores and corresponding familiarity scores to ascertain statistical independence of the two types of scores. Additionally, the percentages of correctly identified new words were analyzed for the "sleep/wake" and "night-half" factors. A minimum of 33% (chance level) correctly identified "new" words was required for a subject to be included in the analysis. All subjects met this criterion. Pairwise comparisons were specified with t-tests. The significance level was set to $\alpha = 0.05$.

Standard polysomnographical recordings of sleep were scored offline according to the criteria by Rechtschaffen and

Kales (1968). For each 30-sec epoch of recording, the sleep stage was determined (W, wake; S1–S4, sleep stage 1–4; REM sleep). Sleep onset was defined by the occurrence of the first epoch of S1 sleep, followed by an epoch of S2 sleep. Total sleep time and the percentages of each sleep stage were determined, with SWS being the sum of S3 and S4. Polysomnographic recordings from the late night of two subjects were incomplete due to technical failure, and were therefore not included in the sleep analysis. Saliva samples for the determination of cortisol were stored at −20°C until assay by use of conventional radioimmunometric assay. Cortisol secretion during each retention interval was estimated by the mean value of the samples obtained immediately before and after the interval. The data from one subject were incomplete as a result of insufficient amount of saliva in some samples; therefore, this analysis contained 11 subjects in the sleep group. Analysis of sleep and cortisol data also relied on ANOVA.

Acknowledgments

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