Effects of Partial Sleep Deprivation on Within-Format and Cross-Format Priming

Gérardine Rauchs, PhD; Karine Lebreton, PhD; Françoise Bertran, MD; Alice Pélérin, MSc; Patrice Clochon, PhD; Pierre Denise, MD; Jean Foret, PhD; Béatrice Desgranges, PhD; Francis Eustache, PhD

1Inserm E0218 – Université de Caen, Basse-Normandie; 2Service des Explorations Fonctionnelles Neurologiques, CHU de Caen; 3Ecole Pratique des Hautes Etudes, Université René Descartes, Paris, France

Study Objectives: The purpose of this study was to examine the effects of sleep on long-term priming. We report the results of a preliminary experiment that enabled us to verify that priming can last for 4 hours, and we also report the results of a study of partial sleep-deprivation.

Design: Subjects performed 2 tasks: within-format and cross-format priming.

Settings: Sleep laboratory.

Participants: Ninety-eight healthy young subjects participated in the 2 studies reported here: 48 in the preliminary experiment and 50 in the sleep-deprivation study.

Intervention: Testing after a 4-hour diurnal retention interval (Experiment 1) or after an equivalent interval filled with early or late sleep, or corresponding periods of wakefulness (Experiment 2).

Measurements and Results: A tachistoscopic identification paradigm, consisting of naming aloud briefly flashed drawings, was used to assess 2 priming conditions: a same-format or within-format condition (in which items were drawings in the study and test phases) and a different- or cross-format condition (in which the symbolic format of the items differed between the 2 phases: words/drawings). In Experiment 1, we revealed significant priming effects in both conditions after a 4-hour interval. In Experiment 2, only same-format priming effects were observed, but their magnitude was smaller than in Experiment 1. There was no significant difference in priming scores between the sleep and wake groups.

Conclusions: Sleep does not appear to have a strong effect on priming. Instead, priming appears to be affected by circadian influences.

Keywords: Priming, partial sleep deprivation, REM sleep, slow-wave sleep, implicit memory, perceptual representation system, semantic memory

Citation: Rauchs G; Lebreton K; Bertran F et al. Effects of partial sleep deprivation on within-format and cross-format priming. SLEEP 2006;29(1): 58-68.
authors found that subjects who had slept during the second half of the night gave significantly more items belonging to the initial list than did those who had slept during the first half of the night. Thus, it appears that REM sleep facilitates the consolidation of implicit information. Nevertheless, the choice of a completion task was perhaps inappropriate, as this task is often contaminated by processes other than implicit ones. The involvement of REM sleep in priming, however, has been confirmed by the same group in a study using nonverbal material (unknown faces). Studies assessing the effects of sleep stages on priming effects are thus relatively scarce but have provided concordant results in favor of the beneficial role of REM sleep in the consolidation of implicit information.

The present study set out to confirm, by means of a previously validated partial sleep deprivation paradigm, that priming benefits from REM sleep. The originality of our design lay in the use of a tachistoscopic identification paradigm, previously developed and validated in a positron emission tomography activation study by Lebreton et al. By means of this tachistoscopic identification paradigm, which optimally limits the involvement of explicit processes, we investigated 2 priming conditions that differed according to whether or not the symbolic format of the items changed between the study and test phases and according to the nature of the instructions given to the subjects. In the same-format condition (drawing/drawing), subjects were instructed to perform physical processing of pictures (perceptual encoding) in the study phase, whereas in the different-format priming condition (word/drawing), they were instructed to perform elaborate processing of words (semantic encoding).

Prior to the partial sleep deprivation study itself (Experiment 2), we report the results of a preliminary behavioral experiment (Experiment 1) intended to demonstrate that both within-format and cross-format priming can last for 4 hours. All subjects gave their consent to the study after detailed information was provided to them, and the study was conducted in accordance with the Declaration of Helsinki.

**EXPERIMENT 1**

**Material and Methods**

**Subjects**

The study cohort consisted of 48 healthy young subjects aged between 18 and 22 years (mean ± SD: 19.5 ± 1.1 years, 45 women) who were divided into 2 groups. There was no significant age difference between these 2 groups (same-format group: n= 24, mean age ± SD: 19.5 ± 1 years, 22 women versus different-format group: n= 24, mean age ± SD: 19.5 ± 1.2 years, 23 women).

**Memory Testing**

In order to avoid the involvement of explicit processes, subjects were told that they were taking part in a study dealing with the perception of words and drawings. No allusion was made to the fact that it was actually a study of memory. Moreover, the different tasks (study and test phases) were presented as entirely separate tests to prevent subjects from establishing a link between the 2 phases.

The long-term priming task used in this study was a tachistoscopic identification paradigm comprising a study phase and a test phase. This paradigm had previously been validated in a positron emission tomography activation study carried out—with a shorter interval between the 2 phases—in our laboratory. The task consisted of naming aloud briefly flashed achromatic line drawings of everyday living or nonliving objects selected from the picture databases developed by Snodgrass and Vanderwart and Gaillard et al. (see reference 20 for further details). For each subject, the presentation time of the stimuli was chosen beforehand on the basis of a selection session, using different drawings from those that were going to be used in the following phases, so that their baseline performance (i.e., for drawings they had never seen before) was between 20% and 40% correct names. The procedure for this session consisted of the successive presentation of 8 lists of 20 drawings. The presentation time for each list varied according to the subject’s performance. Subjects performed 1 of the 2 following priming conditions: same-format (or within-) format or different- (or cross-) format. In the same-format condition, the stimuli retained the same symbolic format between the study and test phases, whereas in the different-format condition, the items took the form of printed words during the study phase and drawings in the test phase (see Figure 1 for an illustration of these tasks).

During the study phase, in the same-format condition, subjects saw 65 drawings presented for 3 seconds with a 500-millisecond interstimulus interval. The 65 drawings included 30 target items for the priming task (test phase), 30 target items for the subsequent recognition task, and 5 distracter drawings—3 at the beginning of the list and 2 at the end—used to avoid primacy and recency effects. Subjects were instructed to decide if a drawing was facing right, left or to the front (neutral position). This orientation task was supposed to induce perceptual processing of the items. In the different-format condition, subjects were shown 65 words, each for 5 seconds (60 targets—30 for the priming task and 30 for the recognition—and 5 distracters), on which they carried out a semantic processing. They were instructed to read each word aloud, indicate its semantic category, and give 1 or several features of the word, preferably functional features. In order to avoid mental repetition of the items that might lead to intentional encoding of the items, a 2-minutes counting backward task was administered after the study phases.

In the test phase, conducted after a 4-hour retention interval filled with diurnal wakefulness, 60 drawings were shown successively in the center of the screen for the amount of time determined beforehand in the selection session. A meaningless mask presented for 500 milliseconds followed each drawing, and thereafter the screen remained blank for 2.5 seconds. The subjects named the drawings or said the word pass. Among the drawings, 30 were studied items (targets), and 30 were nonstudied drawings (controls). In the same-format condition, the target drawings were the drawings that had been previously processed, and, in the different-format condition, the target items were the drawings that corresponded to the words that had been studied.

For each condition, the mean percentage of correct names for target and control drawings was calculated. Priming was attested by significantly better identification of the target items than of the control ones.

The tachistoscopic identification paradigm was followed by a recognition task. This consisted of determining if the drawings presented on the screen had previously been seen or not. Subjects saw a fixation cross for 2 seconds, after which 60 drawings (30 targets from the study list and 30 new items) were presented for
3 seconds with a 500-millisecond interstimulus interval. In the same-format condition, subjects had to decide if they had seen the drawings on the screen during the study phase. In the different-format condition, they had to indicate whether the drawings corresponded to the words presented in the study phase. The presentation time, determined during a preliminary selection phase, was specific to each subject. This test phase corresponds to the same-format condition, since the items are presented during the study and test phases in the same format as they had been in the study (picture-picture). (4) In the second test phase, a series of 60 drawings were presented. Half of them corresponded to the words seen in the study phase (2) and the others were new items. This test phase corresponds to the different-format condition since the items are presented in a different format as they had been in the study phase (word – picture). The presentation time used was the same as during the first test phase. The lists presented were counterbalanced across subjects, each condition being composed of different items.

According to the group to which they belonged, subjects performed the study phases at either 10:45 PM (for the early sleep and early sleep deprivation groups) or at 3:00 AM (for the late sleep and late sleep deprivation groups). Test phases were administered at 3:15 AM for the first 2 groups and at 7:30 AM for the last two.

The drawings used in this illustration were taken from the picture database developed by Gaillard et al (1998).

Figure 1—The tachistoscopic identification tasks. This figure illustrates the 2 priming conditions: same- and different-format. The following explanations concern relate above all to the partial sleep deprivation study (Experiment 2), but the principle is the same for the first study, except that, in Experiment 1, each group of subjects performed only 1 priming condition and that the number of items presented during the study phases was higher due to the presence of a recognition task.

(1) The subjects first performed a study phase consisting in determining the left or right orientation of 35 drawings presented on a computer screen. (2) After that, they performed a second study phase in which they had to read 35 words aloud, to indicate their semantic category and to give a few some functional properties. At the end of this second study phase, an interference task (counting backward from three) was administered for 2 minutes in order to prevent subvocal rehearsal processes that might favor the involvement of explicit strategies during the test phase. These study phases were followed by a 4-hour interval filled with early or late sleep, or equivalent periods of wakefulness. (3) After this interval, subjects performed a first test phase in which they had to name the drawing displayed just before a meaningless figure or say the word “pass.” Half of the 60 drawings presented were those seen in the study phase, and half of them were new items. The presentation time, determined during a preliminary selection phase, was specific to each subject. This test phase corresponds to the same-format condition, since the items are presented during the study and test phases in the same format as they had been in the study (picture-picture). (4) In the second test phase, a series of 60 drawings were presented. Half of them corresponded to the words seen in the study phase (2) and the others were new items. This test phase corresponds to the different-format condition since the items are presented in a different format as they had been in the study phase (word – picture). The presentation time used was the same as during in the first test phase. The lists presented were counterbalanced across subjects, each condition being composed of different items.

We hypothesized that significant priming effects would be observed after a 4-hour interval. Nevertheless, the magnitude of priming might be greater in the same-format condition than in the different one.

**Statistical Analyses**

An initial statistical analysis compared the percentages of control and target items identified correctly by each group, by means of an analysis of variance (ANOVA) with 1 group factor (condition: same or different format) and 1 repeated-measures factor.
Priming Effects

An ANOVA with 1 group factor (condition) and 1 repeated-measures factor (item type) was carried out on the data collected for the 2 groups of subjects. This analysis revealed a significant main effect of the type of item ($F_{1,46} = 138.18, P < .0001$), no significant effect of the condition ($F_{1,46} = 0.74, P < .4$), and a significant interaction between these 2 factors ($F_{1,46} = 7.26, P < .01$). Planned comparisons indicated that target items were identified more accurately whatever the condition (see Figure 2a). There was no significant difference between the 2 groups concerning the identification of target items. In contrast, subjects in the different-format condition identified more control items than subjects in the same-format condition ($P < .001$, see Figure 2a), explaining the interaction between item type and condition.

An unpaired $t$ test was then used to compare the magnitude of priming effects in both conditions. Priming effects (difference between the percentages of correctly identified target and control items) were greater in the same-format condition than in the different-format one ($t = 2.69, P < .01$) (see Figure 2b).

Using unpaired $t$ tests, we also compared the magnitude of these priming effects with those observed by Lebreret al.20 (Experiment 1, a similar behavioral study with 24 subjects in each priming condition), after a 2-minute interval. There was no significant difference between priming scores in both conditions, whatever the interval (2 minutes or 4 hours) between the study and test phases (after a 2-minute interval: priming scores in the same-format and different-format conditions: $30.14 \pm 8.1\%$ and $17.78 \pm 10.34\%$, respectively; after a 4-hour interval: $25.7\% \pm 12.1\%$ and $16.1\% \pm 12.5\%$ for the same-format and different-format conditions, respectively, see also Table 1).

Recognition Performance

An unpaired $t$ test was used to compare the magnitude of recognition scores (i.e., hits minus false alarms) in both conditions. Recognition scores were greater in the same-format than in the different-format one ($t = 3.11, P < .01$; data not shown).

Data are presented as mean ± SD. Group A refers to early sleep group, $n=12$; B, late sleep group, $n=14$; C, early sleep deprivation group, $n=12$; D, late sleep deprivation group, $n=12$.
Unpaired t-tests were also used to compare these recognition scores with those observed by Lebreton et al\(^\text{20}\) (Experiment 1), after a 2-minute interval. Correct recognitions (hits minus false alarms) markedly decreased after a 4-hour interval (same-format condition: 83.33% ± 11.1% vs 40.41% ± 28.7% after a 2-minute interval and a 4-hour interval, respectively, \(P < .001\); different-format condition: 81.67% ± 14.5% vs 14.58% ± 28.7% after a 2-minute interval and a 4-hour interval, respectively, \(P < .001\)). Thus, recognition performance appears to worsen as the length of time between the study and test increases.

**Correlation Between Priming Scores and Recognition Scores**

In order to make sure that the priming effects we measured truly reflected the involvement of implicit memory, correlations between priming and recognition scores were computed. Whereas no significant correlation was found between explicit and implicit measures in the different-format condition (\(r = -0.13\); \(P > .53\)), we observed a trend in favor of a positive correlation between implicit and explicit measures in the same-format one (\(r = 0.39\), \(P > .06\)).

Lastly, an analysis of the postexperiment questionnaire revealed that none of the subjects tried to learn the items during the study phases and none of them established a link between the study and test phases.

To sum up, the results of this first experiment indicate that, after a 4-hour period, there was a higher rate of identification for the items that had been studied (targets) than for the ones that had not (controls) (i.e., significant priming effects) and this effect was significantly greater in the same-format condition. Thus, priming effects can last for up to 4 hours without any significant changes in their magnitude, compared with a 2-minute interval. In contrast, explicit performance after incidental encoding declined drastically over time.

**DISCUSSION**

The results of the first experiment revealed priming effects in both conditions (same-format and different-format) after a 4-hour interval but with a greater amplitude for the same-format priming than for the different-format one.

Our results first confirm that same-format priming effects can last more than a few minutes, as was previously demonstrated by Jacoby and Dallas\(^\text{11}\) using a degraded picture-identification task and a 24-hour interval between the study and the test phases (see also references 14 and 23 for similar conclusions with various tasks and intervals). To the best of our knowledge, the effect of time on different-format priming has seldom been investigated (but see reference 24 for a study with a 24-hour interval). Nevertheless, our data indicate that this form of priming can also last for several hours but appears to be more sensitive to the effect of time than is same-format priming. Our results also concur with previous reports showing that changes in the physical features of stimuli between the study and test phases (e.g., words in the study phase and drawings in the test phase) reduce, but do not eliminate, priming.\(^\text{25,26}\)

The difference in the magnitude of priming effects in the 2 conditions could be explained by the fact that the first condition (same-format) mainly involves perceptual processes and so essentially reflects perceptual priming, whereas the different-format condition has a mixed status, involving both perceptual and conceptual (or semantic) processes. The distinction between these 2 forms of priming (perceptual and conceptual) has been previously reported in the literature\(^\text{11}\) and supported by neuroimaging data (see references 12, 27, and 28 for reviews).

More precisely, concerning the fact that changing the physical features of stimuli between the study and test phases reduces the magnitude of priming, it has been suggested that the nature of within-format and cross-format priming may be different. Thus, Hirshman et al\(^\text{20}\) have observed residual priming effects after modifications of the symbolic format of the items between the 2 phases of the task (i.e., cross- or different-format priming), only when the items had been encoded semantically during the study phase. This result suggests that different-format priming would not rely on the analysis of the specific perceptual properties of stimuli and may reflect conceptual priming. In contrast, within-format priming would reflect perceptual priming. This distinction between within-format–perceptual priming and different-format–conceptual priming has been supported by both experimental\(^\text{29,30}\) and neuroimaging\(^\text{20}\) studies.

The comparison of recognition performance obtained in this study with those reported by Lebreton et al\(^\text{20}\) using a 2-minute interval showed that explicit performance, after incidental encoding, appears to decline drastically over time, which is in line with previous reports.\(^\text{15-17}\)

Overall, these data indicate that implicit and explicit processes are well dissociated in our paradigm, since priming effects can last up to 4 hours, whereas explicit performances do not. This point also highlights the quality of this paradigm to assess implicit memory, which is based on a methodology known to limit the involvement of explicit processes (high number of stimuli presented, very short exposure times, rapid rhythm of presentation of the items, and identification tasks rather than production ones; see reference 31). However, we observed a trend, in the same-format condition, in favor of a correlation between recognition performance and priming scores. This correlation could suggest that common processes are involved in the implicit and explicit tasks and could reflect a contamination of priming by explicit memory processes. However, this interpretation is usually given when the priming task relies on the semantic or associative properties of the items (i.e., conceptual priming) rather than on their perceptual features (perceptual priming).\(^\text{32}\) In addition, and as mentioned above, our paradigm is based on a methodology known to limit, as much as possible, contamination by explicit processes (see reference 31). Moreover, as the recognition task has always been administered after the implicit task, the correlation observed may therefore reflect a possible contamination of recognition performance by implicit processes rather than the opposite situation. This correlation cannot reflect the involvement of a strategy of explicit retrieval either, since none of the subjects tried to voluntarily memorize the drawings or established a link between the study and test phase. So, it appears that the priming effects measured after 4 hours mainly reflect the involvement of implicit memory and are not contaminated by explicit retrieval strategies.

To conclude, same-format and different-format priming assessed by means of a tachistoscopic identification paradigm can last for at least 4 hours. This paradigm would therefore appear to be suitable for assessing the effect of partial sleep deprivation on 2 forms of implicit memory.
EXPERIMENT 2

Material and Methods

Subjects

A total of 60 healthy university students (54 women, 6 men; mean age ± SD: 19.8 ± 1.7 years) participated in this study. All were medication free and had a normal sleep-wake cycle (i.e., going to bed between 11 pm and midnight and waking up between 7 AM and 8 AM). None of the participants had any history of sleep disturbances or psychiatric or neurologic disorders. All subjects spent 2 consecutive nights in the sleep laboratory. The first night was used to accustom them to the experimental conditions, including placement of electrodes. Three subjects were excluded due to technical problems during electroencephalogram recording. Seven subjects were excluded a posteriori (i.e., after the experimental night) due to poor sleep efficiency (< 80%) or because their first half night was dominated by REM sleep or, conversely, because SWS prevailed during the second half night. Finally, 50 subjects (47 women, 3 men, mean age ± SD: 19.6 ± 1.3 years) were included in this study and divided into 4 groups. There was no significant age difference between the groups (data not shown).

Study Design

This experiment took place in the sleep laboratory of Caen University Hospital. The procedure followed in this study was similar to that described and illustrated in our previous study. After an adaptation night, all subjects reported to the sleep laboratory at 7:30 PM. After electrodes had been attached to record their sleep, they were divided into the following groups: 2 sleep groups and, to assess general sleep effects and measure circadian influences, 2 wake controls (sleep-deprivation) groups.

In the early sleep group (n= 12, all women; Group A), subjects started the study phase at 10:30 PM (lasting 20 minute). Thereafter, they went to bed and lights were switched off at 11.00 PM. Four hours after going to bed—a period during which SWS normally prevails—subjects were woken up. To dissipate most sleep-inertia effects, the test phase took place after a 15-minute interval after they had woken up, during which subjects were kept seated in their bed, with the lights on, talking with the experimenter. After this short period, they were invited to perform the test phase of the priming experiment and were then allowed to sleep until 7:00 AM.

In the late sleep group (n= 14, 2 men; Group B), after sleeping for 4 hours (lights out at 10:45 PM), subjects were woken up and, 15 minutes later, performed the study phase of the task (between 3 am and 3:20 AM). Thereafter, they went back to bed to sleep for a further 4 hours—a period normally dominated by REM sleep. Fifteen minutes after they woke up, the test phase was administered.

For subjects in the early sleep deprivation group (n= 12, all women; Group C) and late sleep deprivation group (n= 12, one man; Group D), the procedure was exactly the same as for the corresponding sleep groups, except that the 4-hour interval between the 2 phases was filled with wakefulness instead of sleep. As in the late sleep group, the 4-hour interval of wakefulness in the late sleep deprivation group was precede by 4 hours of sleep. Wakefulness was not monitored using electroencephalography, but, to remain awake without too much cognitive or emotional strain, subjects were allowed to play games or watch television with the experimenter.

Sleep Recording

After an adaptation night in the sleep laboratory, sleep was assessed by standard polysomnography, including electroencephalogram, electrooculogram, and electromyogram. Recordings were scored off line according to Rechtschaffen and Kales criteria. For each 4-hour interval, total sleep time, sleep-onset latency, sleep efficiency, and the time and percentages of time spent in sleep stages 1, 2, 3, 4, and REM sleep (relative to total sleep time) were determined. Time spent in SWS was calculated as the total amount of time spent in sleep stages 3 and 4. Sleep data (percentage of SWS and REM sleep during the retention interval) were also correlated, using Pearson correlation test, with priming scores (in same-format and different-format conditions) for subjects in the 2 sleep groups (Groups A and B).

Memory Testing

The priming tasks used in this second experiment were exactly the same as those used in Experiment 1, except that all the subjects successively performed both priming conditions (same-format and different-format). In addition, items used in Experiment 1 for the recognition tasks were removed, so subjects saw 35 drawings (30 targets and 5 distractors) in the study phase of the same-format condition and 35 words in the different-format condition. As had been done in Experiment 1, a 2-minute counting backward task was administered after the 2 study phases. Conditions were counterbalanced across subjects. In order to cut down the testing time as much as possible and because the results of the first experiment indicated that the priming effects that we measured truly reflected the involvement of implicit memory, the recognition task was not administered here.

Statistical Analyses

An initial statistical analysis involving unpaired t tests was used to check that the retention intervals of Groups A and B were indeed dominated by SWS and REM sleep, respectively. Next, we searched for overall priming effects across all the subjects using an ANOVA with 2 repeated-measures factors (condition and item type). We then looked for a differential effect of sleep and wakefulness on priming by means of an ANOVA with 1 group factor (sleep vs wake) and 2 repeated-measures factors (condition and item type). Lastly, we sought to establish correlations between priming scores (in both conditions) and the amount of SWS and REM sleep in the sleep groups.

RESULTS

Sleep Data

Sleep data recorded during the retention interval for Groups A and B (i.e., during the first and the second halves of the night, respectively) were compared using unpaired t tests. As expected, sleep architecture during these periods substantially differed between the 2 groups with respect to SWS and REM sleep (see Table 2). SWS constituted more than 40% of the retention interval for subjects in Group A (early sleep group) whereas REM
sleep represented only 10% of this period. As for Group B (late sleep group), REM sleep prevailed during the retention interval, constituting more than 27% of sleep, whereas SWS covered only 18% of this period. The amounts of SWS and REM sleep differed significantly between Groups A and B (P < .0001 for both sleep stages). Differences in the other sleep stages were not significant. Total sleep time, sleep latency, and sleep efficiency were similar for both groups.

### Priming Effects

In order to search for overall priming effects, we performed an ANOVA with 2 repeated-measures factors (condition: same-format or different-format; item type: target or control) for all 50 subjects. This analysis revealed a significant main effect of the item type (F₁,₄₉ = 11.78; P < .001), a significant effect of the condition (F₁,₄₀ = 10.33, P < .01), and a significant interaction between these 2 factors (F₁,₄₀ = 8.94, P < .01). Planned comparisons indicated that subjects identified target items more accurately than controls in the same-format condition (P < .001). By contrast, there was no significant difference concerning the percentages of correctly identified target and control items in the different-format condition (see Figure 2c). In addition, while control items were identified equally successfully in both conditions, the percentage of correctly identified target items was higher in the same-format condition than in the different-format one (P < .001) (see Figure 2c). Therefore, our data indicate that priming exists only in the same-format condition (see Figure 2d).

### Effects of Sleep as Compared With Wakefulness

Data were then compared between the sleep and wake groups. For this purpose, an ANOVA with 1 group factor (sleep vs wakefulness) and 2 repeated-measures factors (item type and condition) was performed. This analysis did not reveal any significant effect of group (F₁,₄₀ = 0.5, P > .48) but showed a significant effect of item type (F₁,₄₀ = 11.55, P < .001) and condition (F₁,₄₀ = 10.12, P < .01). The interactions between group and condition as well as the one between group and item type were not significant (F₁,₄₀ = 2.43, P > .12 and F₁,₄₀ = 1.51, P > .22 respectively). In contrast, the interaction between condition and item type was significant (F₁,₄₀ = 8.78, P < .005). Planned comparisons indicated that, in the sleep group (i.e., Groups A and B), target items were identified more accurately than control ones in the same-format condition (F₁,₄₀ = 20.41, P < .001) but not in the different-format one (F₁,₄₀ = 0; P > .99). In the wake group (i.e., Groups C and D), there was no significant difference in the percentages of correctly identified target and control items, whatever the condition (same-format condition: (F₁,₄₀ = 3.12, P > .08; different-format condition: (F₁,₄₀ = 0.08, P > .78). However, percentages of correctly identified target and control items did not differ between the sleep and wake groups, whatever the condition, excepted a trend in favor of a better identification of the target items, in the same-format condition, in the sleep group compared with the wake one (F₁,₄₀ = 3.65, P > .06; see Figure 3).

These last results led us to perform another analysis comprising only data of the same-format priming condition, since obviously different-format priming is not affected by sleep or wakefulness. Thus, we carried out a new ANOVA with 1 repeated-measures factor (item type) and 1 group factor (group: sleep vs wakefulness). This analysis revealed a main effect of the item type (F₁,₄₀ = 19.38, P < .001), but not of the group (F₁,₄₀ = 1.79, p > .18), and a trend in favor of an interaction between these factors (F₁,₄₀ = 3.45, p < .07).

---

**Table 2—Sleep Parameters During the Retention Intervals**

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Early sleep (group A)</th>
<th>Late sleep (group B)</th>
<th>t</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sleep stage, min (% of TST)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>21.5 ± 9.3 (8.5 ± 4.1)</td>
<td>27.1 ± 11.2 (12.1 ± 4.9)</td>
<td>-1.37</td>
</tr>
<tr>
<td>2</td>
<td>87.6 ± 16.9 (38.9 ± 7.4)</td>
<td>93.2 ± 14.2 (42.1 ± 7)</td>
<td>-0.93</td>
</tr>
<tr>
<td>SWS</td>
<td>94.5 ± 17.8 (42 ± 7.3)</td>
<td>40.7 ± 11.4 (18.1 ± 4.4)</td>
<td>9.34***</td>
</tr>
<tr>
<td>REM</td>
<td>23.8 ± 12.7 (10.6 ± 5.6)</td>
<td>61.6 ± 11.4 (27.6 ± 4.1)</td>
<td>-7.98***</td>
</tr>
<tr>
<td>TST, min</td>
<td>227.4 ± 12.8</td>
<td>222.5 ± 18.7</td>
<td>-1.56</td>
</tr>
<tr>
<td>Sleep latency, min</td>
<td>18.9 ± 8.8</td>
<td>25 ± 10.8</td>
<td>0.76</td>
</tr>
<tr>
<td>Sleep efficiency, %</td>
<td>91.4 ± 4</td>
<td>89.9 ± 6.1</td>
<td>0.71</td>
</tr>
</tbody>
</table>

Data are presented mean ± SD. For the early sleep group (Group A, n= 12), sleep parameters were calculated for the first half of the night. For the late sleep group (Group B, n= 14), we used data for the second half of the night. Data were analyzed using unpaired t tests. TST refers to total sleep time; SWS, slow-wave sleep; REM, rapid eye movement sleep. ***: p<0.001.

---

*SLEEP, Vol. 29, No. 1, 2006*
significant correlation between the amount of SWS or REM sleep during the retention interval. Our data revealed significant priming effects after a 4-hour interval: 1.21, P > .32; different-format condition: F_{1,46} = 0.25, P > .86) (see Figure 4 and Table 1). These data also highlighted the great intersubject variability within each group.

Correlations Between Priming Scores and Percentage of Sleep Stages

Pearson correlations were computed on the following variables: priming scores in the same-format or different-format condition and the amount of SWS or REM sleep during the retention interval. These correlations were performed, first, for the whole sleep group (i.e., groups A and B) and, second, separately for Groups A and B, taking into account sleep data for the first half of the night for Group A and for the second half of the night for Group B. No significant correlation between the priming score and the amount of SWS or REM sleep was found whatever the condition (see Table 3).

DISCUSSION

Our data revealed significant priming effects after a 4-hour interval but only in the same-format condition. Furthermore, the amplitude of priming effects did not differ between the 4 groups (early and late sleep groups and control wake groups). Finally, no significant correlation between the amount of SWS or REM sleep and the priming scores was found, whatever the priming condition.

In this experiment, priming was only detected in the same-format condition. This result differs from those of the first experiment, in which priming was observed in both conditions after a diurnal 4-hour interval. The paradigm used here was based on a tachistoscopic presentation of stimuli that required a sustained level of attention. Attentional abilities are not required for priming per se but were engaged in this task due to the very short exposure times of the items. In this experiment, subjects were tested in fairly unfavorable circadian conditions, and it is likely that both their attentional abilities and their perceptual processes were less efficient than they would have been in diurnal testing (see references 34 and 35 for reviews). This may explain why the performances obtained during the night were lower than those obtained during the day. Furthermore, the overall decrease in performances when subjects were tested during the night made it impossible to detect different-format priming. Thus, the superiority of same-format priming over different-format priming reported in Experiment 1 was confirmed by the data from the second experiment, which corresponded here to a disappearance of priming in the different-format condition.

The fact that we observed priming in the same-format condition but not in the different-format one supports the idea that these 2 conditions could reflect 2 different forms of priming. Indeed, based on experimental and neuropsychological data, 2 forms of priming have been identified and are assumed to reflect the operations of different brain systems. Thus, perceptual priming may be subserved by a cortically based, presemantic perceptual representation system, which processes and represents information about the form and structure of the stimuli but not about their meaning or associative properties. In contrast, conceptual priming may depend on the modification or addition of new information in semantic memory. This distinction has also been underpinned by functional imaging studies (see references 12, 27, and 28 for reviews). Thus, perceptual priming is usually accompanied by a decrease in regional cerebral blood flow in some posterior cortical areas, whereas conceptual priming tasks tend to lead to decreases in regional cerebral blood flow in frontal areas. However, the distinction between these 2 forms of priming is not so clear and easily measurable. Semantic processes can be involved in tasks used to assess perceptual priming, and, conversely, perceptual processes can be engaged in conceptual priming tasks.

Several studies of perceptual priming have shown a dissociation between priming and explicit memory in healthy subjects. As this dissociation is harder to obtain with conceptual priming tasks, one can suppose that our different-format condition was more likely than the same-format one to favor the involvement of explicit processes. However, this kind of contamination by explicit processes appears rather unlikely, as we did not find any significant correlation in the first experiment between priming scores and explicit performance in the 2 priming conditions.

The comparison between the sleep versus wake groups did not reveal any beneficial effect of sleep on both different-format and same-format priming even if the effect of sleep on same-format priming is less clear cut. Thus, our data do not allow us to conclude in favor of a clear and strong effect of sleep on this particular form of priming. Nevertheless, an analysis comprising only the data of the same-format condition has shown a trend in favor of an interaction between the item type and the group (that is, a better identification of target items compared with control ones in subjects who slept), but this trend does not reach significance.
even if we add more subjects. It appears therefore that, on this particular (and pure) perceptual priming task, we cannot provide any firm conclusion in favor of a beneficial effect of sleep, and, if sleep plays a role in this phenomenon, this one may be limited because the percentage of correct identification of target items differs by less than 10% between sleep and wake groups (identification of control items being equivalent in both groups), a difference that appears negligible.

The lack of any significant difference between the 4 groups may be explained, in part, by the great intersubject variability within each group, often observed in priming studies. It is unlikely, however, that sleep inertia accounts for this result. Indeed, sleep inertia would normally result in poorer performances by the sleep groups compared with the sleep-deprived ones. However, this is not what we observed, as performances were equivalent among all groups. Accordingly, even though sleep inertia can last up to 30 minutes (see reference 41 for review), the 15-minute interval proposed between awakening and testing would appear to have been sufficient to dissipate most sleep inertia effects. These results suggest that consolidation of this implicit learning is not enhanced by sleep. This observation is supported by the lack of any significant correlation between priming scores and the amount of SWS or REM sleep during the retention interval.

Our results do not concur with those previously reported in the literature using a word-stem completion task, which provided evidence in favor of a beneficial effect of REM sleep on priming. These discrepancies can probably be explained by methodologic reasons (notably the instructions given to the subjects) and by the fact that the word-stem completion task is neither purely perceptual nor entirely conceptually driven and consequently does not specifically assess the perceptual representation system. Wagner et al have also investigated the impact of nocturnal sleep on implicit memories using visual stimuli (faces), as in the present study. In their article, the authors describe 2 experiments, but only 1 of them highlighted classic priming effects (i.e., shorter reaction times for previously encountered faces than for new ones) and the beneficial effect of REM sleep. In the study phase of this experiment, subjects had to indicate the sex of the faces presented to them by pressing keys as quickly as possible and then, in the test phase, decide whether a face was familiar or not. Thus, priming was evidenced only in a situation in which the instructions given to the subjects clearly encouraged them to refer to a previous event. In that sense, the task involved explicit processes rather than implicit memory. Lastly, another explanation for the discrepancy between Plohal and Born’s results and ours could be that these authors used only men for their study, whereas our subjects were mainly women. Nevertheless, to the best of our knowledge, no established male-female differences have been reported using priming paradigms.

Our results are nevertheless in keeping with those reported by Robertson et al, who assessed explicit and implicit sequence learning by means of a serial reaction time task. These authors demonstrated that, contrary to explicit learning, implicit learning does not benefit from sleep. Nevertheless, it is important to bear in mind that this task relied on mechanisms other than priming and led to discrepant conclusions concerning its sleep dependency (see reference 44).

In some respects, the tachistoscopic identification task resembles the visual discrimination task developed by Karni et al. Both tasks are based on very short exposure time for the items.

---

**Table 3**—Correlations Between the Amount of SWS and REM Sleep (Relative to Total Sleep Time) During the Retention Interval and Priming Scores in the Same-Format and Different-Format Conditions

<table>
<thead>
<tr>
<th>Priming Scores</th>
<th>Same-format condition</th>
<th>Different-format condition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sleep group (A + B) SWS</td>
<td>$r = -0.68$ (P = .742)</td>
<td>$r = -0.14$ (P = .49)</td>
</tr>
<tr>
<td>REM</td>
<td>$r = 0.17$ (P = .394)</td>
<td>$r = -0.01$ (P = .959)</td>
</tr>
<tr>
<td>Group A SWS</td>
<td>$r = -0.16$ (P = .622)</td>
<td>$r = 0.06$ (P = .86)</td>
</tr>
<tr>
<td>REM</td>
<td>$r = 0.25$ (P = .428)</td>
<td>$r = -0.34$ (P = .279)</td>
</tr>
<tr>
<td>Group B SWS</td>
<td>$r = 0.24$ (P = .416)</td>
<td>$r = -0.11$ (P = .705)</td>
</tr>
<tr>
<td>REM</td>
<td>$r = 0.17$ (P = .57)</td>
<td>$r = -0.27$ (P = .357)</td>
</tr>
</tbody>
</table>

For Group A, sleep parameters from the first half of the night were used. Conversely, for Group B, data from the second half part of the night were computed. Correlations are first reported for the whole sleep group (groups A + B). $r$ = Pearson’s correlation coefficient.

In a partial sleep deprivation paradigm, Gais et al showed that performance on this task significantly improved after early sleep but that there was a 3-fold improvement after a whole night’s sleep. Stickgold et al also showed that there is no improvement in performance during a day without any sleep episode. These studies therefore suggest that sleep plays a mandatory role in the consolidation of this learning but that a 4-hour interval may be too short to reveal strong memory effects. We cannot exclude the possibility that this was the case of our paradigm and that the retention interval was not sufficient to observe any differential effect of sleep compared with wakefulness.

Peigneux et al suggested that posttraining processing during sleep can only take place if the training experience has generated coherent information to process (i.e., if the material to be learned is structured and a certain level of training has been achieved). During priming tasks, stimuli are presented only once, and the items do not undergo any major process before being stored as representations. Thus, repeated exposure to the items may be necessary if a structured representation is to emerge on which sleep can later act. In this case, priming would not benefit from sleep.

These present results lead us to distinguish between an obligate and an enhancing function of sleep in memory consolidation. Thus it appears here that sleep does not play an obligate role in the consolidation of this particular type of implicit learning, as significant priming effects can be observed after a diurnal 4-hour interval (Experiment 1). Sleep does not appear to have a strong enhancing effect on implicit memory consolidation either, as the performances of the sleep groups did not differ from those of the wake groups tested in similar circadian conditions of testing.

To conclude, our present results suggest that different-format priming is not differentially affected by sleep and wakefulness. As for the same-format condition, our particularly pure paradigm did not allow us to clearly conclude in favor of a beneficial effect of sleep on perceptual priming. In contrast, it appears that both forms of priming are instead affected by circadian influences (i.e., are stronger during the day than at night). Thus, our data indicate that when subjects are tested late in the evening or in the middle of the night, same-format priming (taping predominantly perceptual processes) is revealed, albeit to a lesser degree compared with diurnal performance, whereas different-format priming (tap-
REFERENCES

43. Herlitz A, Nilsson LG, Backman L. Gender differences in episodic...
44. Robertson EM, Pascual-Leone A, Press DZ. Awareness modifies the
45. Peigneux P, Laureys S, Fuchs S, et al. Learned material content and
acquisition level modulate reactivation during posttraining rapid-
46. Peigneux P, Laureys S, Delbeuck X, Maquet P. Sleeping brain,
learning brain. The role of sleep for memory systems. NeuroReport