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The impact of post-learning sleep vs. wakefulness on recognition memory for faces with different facial expressions

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Abstract

A beneficial effect of sleep after learning, compared to wakefulness, on memory formation has been shown in many studies using a variety of tasks. However, none of these studies has specifically addressed recognition memory for faces so far. The recognition of familiar faces, together with the extraction of emotional information from facial expression, is a fundamental cognitive skill in human everyday life, for which specific neural systems and mechanisms of processing have been developed. Here, we investigated the role of post-learning sleep for later recognition memory for neutral, happy, and angry faces. Twelve healthy subjects, after judging the emotional valence of the faces in the evening (learning phase), either slept normally in the subsequent night, with sleep recorded polysomnographically (sleep condition), or remained awake (wake condition) according to a cross-over design. Recognition testing took place in the second evening after learning, i.e. after a further night of regular sleep spent at home. Sleep after learning, compared to wakefulness, enhanced memory accuracy in recognition memory. This effect was independent of the emotional valence of facial expression. The response criterion at recognition testing did not differ between sleep and wake conditions. The amount of non rapid eye movement (NonREM) sleep during post-learning sleep correlated positively with memory accuracy at recognition testing, while time in REM sleep was associated with a speeded responding to the learned faces. Results suggest that face recognition, despite its dependence on specialized brain systems, nevertheless relies on the general neural mechanisms of sleep-associated memory consolidation.

Keywords: Sleep; Faces; Recognition memory; Emotion; Explicit; Implicit; NonREM sleep; REM sleep

1. Introduction

Evidence from animal and human studies supports the notion that sleep plays a crucial role in the consolidation of newly acquired memory traces (e.g., Buzsáki, 1998; Pennartz, Uylings, Barnes, & McNaughton, 2002; Stickgold, 2005). In humans, a beneficial effect of sleep on memory retention of previously learned material has been demonstrated for a broad variety of tasks and materials, where specific sleep stages are differentially implicated depending on the memory system addressed by the specific task (Gais & Born, 2004a; Maquet, 2001; Walker & Stickgold, 2006). Regarding the fundamental distinction between hippocampus-dependent explicit (declarative) and hippocampus-independent implicit (nondeclarative) memory (Squire, 1992), the latter appears to benefit mainly from rapid eye movement (REM) sleep, the former from non-rapid eye movement (NonREM) sleep, in particular slow wave sleep (SWS) (Fowler, Sullivan, & Ekstrand, 1973; Karni, Tanne, Rubenstein, Askenasy, & Sagi, 1994; Plihal & Born, 1997, 1999; Tucker et al., 2006; Wagner, Hallschmid, Verleger, & Born, 2003).

The present study investigates the role of sleep in recognition memory for previously seen faces. Faces belong to the most important visual stimuli humans encounter in everyday situations. We usually identify the persons we know by recognizing their face, a process for which specific neuroanatomical systems have developed in the brain

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(Allison et al., 1994; Farah, 1996; Kanwisher, 2000; Tsao, Freiwald, Tootell, & Livingstone, 2006). However, facial stimuli have seldom been used as learning material in sleep research (Clemens, Fabo, & Halasz, 2005; Wagner et al., 2003). Thus, although the ability to reliably recognize familiar faces is one of the most fundamental cognitive skills in human life, little is known so far about how memory for faces is influenced by sleep. In a previous study, we have investigated the effect of sleep on implicit face memory in a reaction time priming task and found evidence for a supporting effect specifically of sleep periods containing high amounts of REM sleep (Wagner et al., 2003). Here, we extend these findings by investigating the role of sleep in *explicit* memory for faces in a standard recognition memory procedure. Explicit recognition of familiar faces is a basic prerequisite for appropriate human social behavior. Importantly, recent findings in other memory tasks indicated that sleep can even be more relevant to explicit than implicit aspects of memory formation (Fischer, Drosopoulos, Tsen, & Born, 2006; Robertson, Pascual-Leone, & Press, 2004; Wagner, Gais, Haider, Verleger, & Born, 2004).

The only study on sleep-associated memory consolidation that used facial stimuli to assess explicit memory so far was reported by Clemens and colleagues (2005), who primarily investigated verbal declarative memory (remembering names) but introduced the face memory task as a nonverbal control task. In this study, subjects learned face-name associations in the evening and were tested after a night of sleep in the next morning for verbal (free recall of the names) and nonverbal memory (face recognition task). Recognition memory for the faces was positively associated with total sleep time and the amount of NonREM sleep during the night (while overnight memory retention of the names correlated with the number of sleep spindles). Here, we compare directly the effects of sleep and wakefulness following learning on subsequent recognition of faces newly encountered at learning. To avoid confounds with circadian factors, learning and memory testing always took place at the same time of day in both conditions.

A second aim of the study was to investigate the possible modulating role of emotional valence on sleep-associated face recognition. Apart from the identification of familiar persons, conveying emotional information via facial expression is the second major function of faces (see Calder & Young, 2005, for a recent discussion of both functions). To vary emotional valence of the learning material, we therefore included faces with neutral, positive (happy), and negative (angry) facial expression. Emotionally valenced material is typically better remembered than neutral material (a phenomenon called "emotional enhancement" in memory) and previous studies indicated that the effect of sleep on memory consolidation can differ depending on the emotional valence of the learning material, with memory consolidation for highly emotional material particularly benefiting from sleep periods containing high amounts of REM sleep (Cahill & McGaugh, 1998; Christianson, 1992; Hamann, 2001; Wagner, Gais, & Born, 2001, 2005). However, because these observations mainly refer to verbal free recall tasks, they do not necessarily hold for face recognition memory. Although emotional enhancement has also been reported for recognition memory tasks (Bradley, Greenwald, Petry, & Lang, 1992; Ochsner, 2000), several studies on recognition memory failed to confirm this and rather found evidence for an emotion-induced shift towards a more liberal response bias, i.e., a general tendency to classify emotional stimuli as familiar regardless of whether they were actually presented previously or not (Joyce & Kutas, 2005; Windmann & Kutas, 2001). This has also been demonstrated specifically for face stimuli (Johansson, Mecklinger, & Treese, 2004). Apart from memory performance per se, this response bias may be also influenced by sleep. We therefore tested effects of post-learning sleep not only on memory accuracy, but also on response bias in recognition memory (see Snodgrass & Corwin, 1988).

2. Materials and methods

2.1. Subjects

Twelve healthy non-smokers (aged 19–30 years, 5 female) served as paid participants in the experiments. They were on no medication, free from any neurological and psychological disorders, and reported a normal sleep-wake cycle. All subjects spent an adaptation night asleep in the sleep laboratory, including the placement of electrodes, before participating in the experiment proper. One subject who displayed an obvious general deficit in face recognition (memory performance did not exceed chance level) was replaced by a new subject.

2.2. General design

The experimental design is depicted in Fig. 1a. Each subject was tested on two experimental conditions (separated by at least two weeks), with the order balanced across subjects. In one condition subjects slept in the night following learning (sleep condition), in the other condition they remained awake (wake condition). Learning always took place in the evening immediately before the sleep or wake night, recognition testing in the evening two days later. This delay allowed a recovery night in the wake condition, preventing unspecific immediate effects of prolonged sleep deprivation on memory performance, which would be expected in this condition if memory was tested on the first day following learning.

In the sleep condition subjects reported to the laboratory at 21:00 h. After the placement of electrodes for sleep recordings the learning phase was conducted (22:30–23:00 h). Immediately afterwards, subjects went to bed and lights were turned off to enable 8 h of sleep (until 7:00 h), which was monitored by standard polysomnography. In the wake condition subjects reported to the laboratory at 22:30 h to perform the learning phase. Afterwards, they remained at the laboratory until 7:00 h in the next morning, kept awake by being involved in conversations, reading and writing emails, or playing simple games (e.g. dice games) with the experimenter.

In both experimental conditions, subjects left the laboratory shortly after 7:00 h in the morning to follow their normal diurnal activities. Recognition testing took place in the second evening after learning at 18:00–18:30 h, allowing subjects to spend a recovery night at home. Daytime sleep (i.e., sleep outside a time window between 21:00 and 11:00 h) was not allowed until subjects returned to the laboratory for recognition testing. In the wake condition, where subjects suffered from sleep deprivation, this requirement was controlled by actimetry (Actiwatch® system, Cambridge Neurotechnology, Cambridge, UK). While very short sleep periods in the order of minutes may sometimes not be detectable with this system, longer periods of sleep can safely be recognized. Subjects also had to protocol

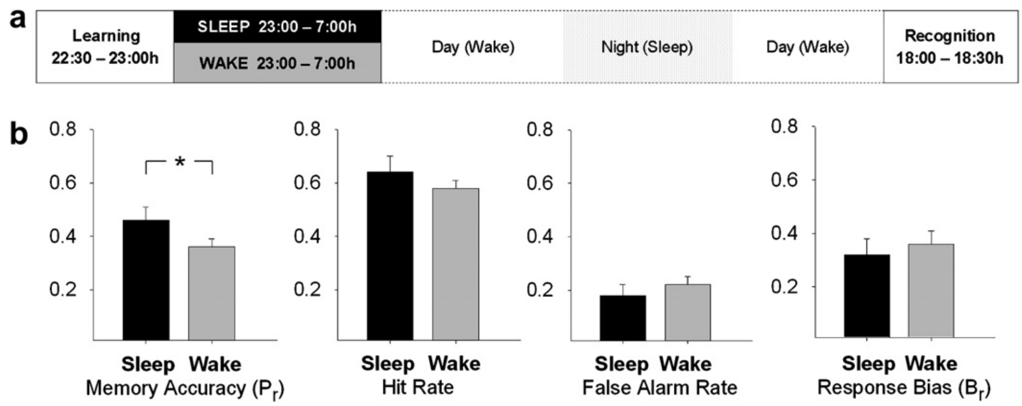

Fig. 1. (a) Experimental design. In the night immediately following learning, subjects in one condition slept and in the other condition remained awake in the laboratory (23:00–7:00 h). A recognition test for the learned faces was performed two days after learning, allowing subjects to spend a night of recovery sleep at home, which served to overcome unspecific effects of sleep deprivation on retrieval performance in the wake condition. (b) Effects of sleep vs. wakefulness in the consolidation night after learning on memory performance in the recognition test, collapsed across all three categories of emotional valence. Post-learning sleep, compared to wakefulness, enhanced memory accuracy (i.e. the difference between hit rate and false alarm rate) in the face recognition task (*$p < .05$).

their activities in a questionnaire until they returned to the laboratory for recognition testing. These data confirmed general adherence to the experimental protocol. In the night spent at home, subjects went to bed in both conditions at about the same time (sleep 23:41 h ± 16 min, wake 23:49 h ± 26 min, $p = .76$), while they got up in the following morning significantly later in the wake than the sleep condition (sleep 8:45 h ± 10 min, wake 9:04 h ± 29 min, $p = .004$). Subjective sleep quality in this night was also judged as significantly higher in the wake compared to the sleep condition (4.25 ± 0.22 vs. 3.42 ± 0.31 on a 5-point scale, $p = .04$).

As an additional control for unspecific effects of general cognitive functioning on memory performance, subjective ratings of sleepiness, activation, concentration, motivation, tension, and boredom were assessed at the beginning of each learning and recognition phase (5-point scales).

2.3. Task and procedure

Colored photographs of faces of 120 individuals (60 men and 60 women) from the "AR face database" (Martinez & Benavente, 1998), an established picture set in face recognition research (e.g., Joyce & Kutas, 2005; Martinez, 2002), served as stimuli for the face recognition task. All faces belonged to persons in young adult age (about 20–40 years) with Caucasian or Hispanic ethnicity. They were randomly assigned to two sets of 60 faces used for the two experimental conditions of a subject. Each of the two sets was subdivided into two parallel subsets of 30 faces, one of which served as learning material for the study phase (learning). These 30 faces ("old" faces) were later presented again at recognition testing, intermixed with the 30 faces from the subset not presented at learning ("new" faces). Each subset consisted of 10 faces displaying a neutral expression, 10 faces displaying a happy expression, and 10 faces displaying an angry expression (with 5 male and 5 female faces in each category). Assignment of the two sets to experimental conditions was balanced across subjects, but within a set always the same 30 faces served as "old" and "new" faces, respectively.

Faces were presented one after the other in the middle of a 17 in. color monitor at a visual angle of about 10°. At learning, subjects had to indicate for each face the emotional valence of facial expression (neutral, happy, or angry) by pressing one of three response keys (with mapping of keys to response alternatives balanced across subjects). No instruction was given to actively memorize the faces during this task. Each face was presented for 5 s, and no time limit was set for responding. To keep encoding time constant for all faces, responding was not possible before the face had disappeared from the monitor. The next face appeared 1 s after the subject had pressed a response key. At recognition testing, subjects had to indicate for each face whether it was "old" (already seen at learning) or "new" (not seen at learning) by pressing one of two response keys (with mapping of keys to "old" and "new" answers balanced across subjects). Presentation time was 1.5 s, with an inter-stimulus interval of 2 s. If a subject did not press a response key within 3 s from stimulus onset (which was abundant time), the trial was regarded as an omission and a warning signal appeared on the screen. Subjects were instructed to answer both as accurately and as fast as possible. This instruction served to limit variability in reaction times without posing major constraints on the decision process in explicit memory search.

2.4. Dependent variables and statistical analysis

Measures of recognition memory were determined according to the two-high threshold model (Snodgrass & Corwin, 1988), including hit rate (HR = proportion of old faces classified as "old"), false alarm rate (FAR = proportion of new faces classified as "old"), the memory accuracy measure P_r [= HR − FAR], and the response bias measure B_r [= FAR/(1 − P_r)]. Moreover, reaction times were recorded because sleep effects can manifest themselves also in speeded responding to old as compared to new items (Wagner et al., 2003). For consolidation sleep recorded in the sleep laboratory, total sleep time, sleep onset latency, and absolute and relative time spent in different sleep stages were determined according to the criteria of Rechtschaffen and Kales (1968). Slow wave sleep (SWS) was calculated as the sum of time in sleep stages 3 and 4, NonREM sleep as the sum of sleep stages 1–4.

Statistical analyses of recognition memory based on a 2 × 3 analysis of variance (ANOVA) including the two within-subjects factors Sleep (sleep/wake) and Emotional Valence (neutral/happy/angry facial expression). Reaction time analyses were performed on correct key presses and included the additional factor Old/New. Ratings of subjective sleepiness, activation, concentration, motivation, tension, and boredom assessed at learning and recognition testing were analyzed by a 2 × 2 ANOVA with the two within-subject factors Sleep (sleep/wake) and Phase (learning/recognition testing). Significant ANOVA main effects or interactions were specified by pairwise t-test comparisons. Where appropriate, degrees of freedom were adjusted according to the Greenhouse–Geisser procedure. Pearson's correlation coefficients were calculated to identify linear relationships between memory measures and single sleep stages.

3. Results

3.1. Face recognition

Results for recognition memory measures (hit rate, false alarm rate, memory accuracy, response bias) are shown in

Table 1
Face recognition

	Sleep		Wake		
	Mean	*SEM*	Mean	*SEM*	*p*
Hit rate					
Angry faces	0.63	0.07	0.59	0.06	.723
Neutral faces	0.69	0.06	0.61	0.05	.117
Happy faces	0.61	0.07	0.53	0.04	.298
All faces	0.64	0.06	0.58	0.03	.266
False alarm rate					
Angry faces	0.09	0.04	0.19	0.04	.082
Neutral faces	0.21	0.05	0.26	0.04	.365
Happy faces	0.24	0.06	0.22	0.04	.754
All faces	0.18	0.04	0.22	0.03	.325
Memory accuracy (P_r)					
Angry faces	0.53	0.08	0.40	0.07	.173
Neutral faces	0.48	0.06	0.35	0.04	.112
Happy faces	0.37	0.07	0.32	0.04	.491
All faces	0.46	0.05	0.36	0.03	**.038**
Response bias (B_r)					
Angry faces	0.18	0.08	0.36	0.08	.204
Neutral faces	0.38	0.09	0.41	0.06	.686
Happy faces	0.39	0.07	0.30	0.06	.383
All faces	0.32	0.06	0.36	0.05	.962

Bold indicates that the value is the only significant pairwise comparison between sleep and wake conditions.

Table 1, including pairwise *t*-tests between sleep and wake conditions. Sleep after learning, compared to wakefulness, generally enhanced memory accuracy (P_r), independent of facial expression (sleep 0.46 ± 0.05 vs. wake 0.36 ± 0.03, $F(1,22) = 5.52$, $p = 0.038$, for main effect of Sleep; $p = .69$ for Sleep × Valence interaction). Although both the hit rates and the false alarm rates contributed to this effect (as indicated by overall higher hit rates and lower false alarm rates after sleep than wakefulness), these measures per se were not significantly affected by sleep overall or in interaction with valence ($p > .26$, for all respective effects). Control analyses, which included the factor "Order" in the ANOVA, showed that the sleep effect on memory accuracy did not depend on whether the sleep condition was the first or second experimental night for a subject ($p = .41$), nor was there an overall order effect ($p = .57$).

Regardless of sleep, both false alarm rates and memory accuracy (P_r), but not hit rates, tended to be influenced by valence ($p = .08$ and .10, respectively, for main effect of Valence on false alarm rates and P_r; $p = .23$ for hit rates), with lower false alarm rates for angry faces as compared to neutral and happy faces and, consequently, highest memory accuracy for angry faces (false alarm rates: angry 0.14 ± 0.03, neutral 0.23 ± 0.04, happy 0.23 ± 0.03; P_r: angry 0.47 ± 0.07, neutral 0.41 ± 0.04, happy 0.34 ± 0.04). The response bias (B_r) was not overall affected by sleep or emotional valence ($p = .64$ and $p = .19$, for respective main effects), while both factors tended to interact in their influence on response bias ($p = .09$) due to a relatively enhanced conservative response bias (i.e., an inclination to answer "new") specifically for angry faces in the sleep condition. Fig. 1b summarizes the results for recognition performance collapsed across the three valence categories.

We additionally performed an analysis in which valence categories were formed on the basis of individual judgments of facial expression rather than by a priori classification. This analysis was performed for hit rates only, because individual judgments of facial expression were only obtained for old faces presented at learning. This analysis revealed the same pattern of results as the analysis of hits based on the a priori classification of valence categories. Although sleep enhanced hit rates numerically compared to wakefulness, this effect did not reach significance (sleep 0.66 ± 0.06 vs. wake 0.57 ± 0.03, $p = .12$, for main effect of sleep). Valence did not affect hit rates overall or in interaction with sleep ($p > .30$).

3.2. Reaction times

Reaction time data are displayed in Table 2. Sleep did not exert a substantial effect on reaction times overall or in interaction with valence or the Old/New factor ($p > .13$, for all effects). Also, reaction times did not differ on the whole between old and new faces ($p = .35$ for main effect Old/New). A significant main effect of Valence ($p = .04$) indicated that across all conditions responses were generally faster for neutral as compared to happy and angry faces (neutral 857 ± 24 ms, happy 889 ± 20 ms, angry 883 ± 20 ms; $p = .003$, for neutral vs. happy; $p = .07$, for neutral vs. angry faces). Whereas the data in Table 2 show that this effect results mainly from the strong differences in this direction in the Old/Wake and the New/Sleep subconditions, Valence did not interact significantly with the two other factors ($p = .69$, for Valence × Old/New interaction; $p = .19$, for Valence × Sleep interaction; $p = .14$, for Valence × Old/New × Sleep interaction).

3.3. Sleep

Two participants, whose sleep could not be recorded completely due to technical problems, were excluded from

Table 2
Reaction times (ms)

	Sleep		Wake		
	Mean	*SEM*	Mean	*SEM*	*p*
Old					
Angry faces	848	40	949	31	.113
Neutral faces	876	31	846	38	.577
Happy faces	905	31	899	24	.878
All faces	876	25	898	25	.709
New					
Angry faces	851	27	883	35	.314
Neutral faces	822	36	884	36	.112
Happy faces	853	33	899	44	.365
All faces	842	29	889	36	.174
Difference old–new					
Angry faces	−3	34	66	43	.225
Neutral faces	53	47	−38	33	.174
Happy faces	52	48	−1	48	.494
All faces	34	29	9	33	.584

sleep analysis. Polysomnographic recordings from the remaining subjects confirmed a normal distribution of sleep stages during consolidation sleep in the night after learning (stage 1 sleep, $3.2 \pm 1.0\%$, stage 2 sleep, $59.3 \pm 2.6\%$, SWS $18.7 \pm 2.5\%$, REM sleep $17.4 \pm 1.17\%$, wake time $0.3 \pm 0.1\%$, total sleep time 441.8 ± 4.8 min, sleep onset 11.5 ± 2.4 min).

Correlations between recognition performance and sleep parameters showed that in the sleep condition overall memory accuracy was strongly correlated with the amount of NonREM sleep during consolidation sleep ($r = .79$, $p = .007$; Fig. 2a). Hit rate or false alarm rate alone were not significantly associated with NonREM sleep ($r = .36$, $p = .31$, and $r = -.42$, $p = .23$, respectively). Separate analyses for the three valence categories of facial expression revealed that the association between memory accuracy and NonREM sleep was significant for angry and happy, but not neutral faces (angry: $r = .79$, $p = .006$, happy: $r = .86$, $p = .001$, neutral: $r = .03$, $p = .93$). The same pattern, although less pronounced, was found for the correlation between memory accuracy and total sleep time in the night after learning (all faces: $r = .65$, $p = .042$, happy faces: $r = .66$, $p = .037$, angry faces: $r = .61$, $p = .063$, neutral faces: $r = .11$, $p = .76$), but not for any of the single sleep stages within NonREM sleep (S1, S2, S3, S4, and SWS). REM sleep, in contrast to NonREM sleep, was negatively correlated with memory accuracy, although not significantly ($r = -.53$, $p = .116$) and tended to be associated with higher overall false alarm rates ($r = .59$, $p = .072$).

Regarding reaction times, there was a strong negative correlation between REM sleep and reaction times for old faces ($r = -.76$, $p = .012$), but not for new faces ($r = -.02$, $p = .95$). Consequently, REM sleep was also associated with the difference between old and new faces in reaction times as an indicator of implicit memory ($r = -.70$, $p = .024$; Fig. 2b). This pattern was observed in all three valence categories, but did not reach significance in separate analyses for the three categories (angry: -0.54, $p = .108$, happy: -0.54, $p = .108$, neutral: -0.59, $p = .071$). Neither NonREM sleep overall nor any sub-stage of NonREM sleep correlated significantly with any reaction time measure.

3.4. Subjective ratings

Ratings of subjective sleepiness, activation, motivation, boredom, concentration, and tension obtained at learning and recognition testing did not differ between sleep and wake conditions (sleep vs. wake means ± SEM at learning: sleepiness 3.08 ± 0.26 vs. 2.42 ± 0.31, activation 2.83 ± 0.35 vs. 3.25 ± 0.31, motivation 3.08 ± 0.38 vs. 3.42 ± 0.36, boredom 2.25 ± 0.33 vs. 2.00 ± 0.28, concentration 2.92 ± 0.38 vs. 3.42 ± 0.26, tension 2.25 ± 0.31 vs. 2.08 ± 0.29; at recognition testing: sleepiness 1.58 ± 0.26 vs. 1.92 ± 0.36, activation 3.83 ± 0.31 vs. 3.58 ± 0.23, motivation 3.67 ± 0.28 vs. 3.25 ± 0.18, boredom 2.17 ± 0.24 vs. 1.92 ± 0.23, concentration 3.42 ± 0.26 vs. 3.42 ± 0.19, tension 2.08 ± 0.34 vs. 2.00 ± 0.30; $p > .19$, for all main effects of Sleep and Sleep × Phase interactions). Independent of sleep vs. wake conditions, there was a general tendency to feel less sleepy and more activated at recognition testing than at learning (sleepiness, $p < .01$, activation, $p < .05$, for main effect of Phase), which probably reflects circadian influences as well as anticipatory effects (recognition testing, in contrast to learning, was not followed by an overnight stay at the laboratory).

3.5. Performance at learning

To control for possible "baseline" differences in facial processing, we compared experimental conditions also with respect to task performance at learning. Identification of facial expression did not differ between sleep and wake conditions (means ± SEM for sleep vs. wake conditions: angry faces, $39.2 \pm 2.6\%$ vs. $37.5 \pm 3.5\%$; neutral faces, $76.7 \pm 3.3\%$ vs. $78.3 \pm 2.7\%$; happy faces $94.2 \pm 2.3\%$ vs. $94.2 \pm 2.6\%$; $p = .99$, for main effect of Sleep; $p = 0.92$, for Sleep ×

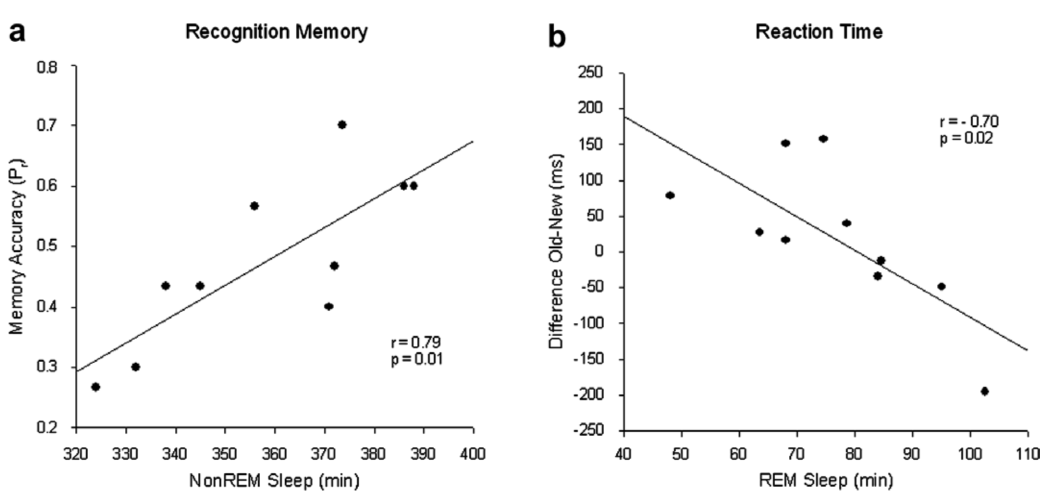

Fig. 2. Time spent in NonREM and REM sleep during post-learning consolidation sleep are differentially correlated with explicit and implicit aspects of memory performance at recognition testing. NonREM sleep was associated with memory accuracy in recognition memory, i.e. explicit memory for the faces (a), while REM sleep was associated with a relative speeding of response time for old as compared to new faces, i.e. repetition priming (implicit memory) (b).

Valence interaction). Independent of experimental sleep vs. wake conditions, identification of facial expression (as defined by the a priori valence categories) was distinctly better for neutral and happy faces as compared to angry faces and better for happy as compared to neutral faces ($p < .001$, for main effect of Valence and all pairwise comparisons).

4. Discussion

The present study investigated the role of sleep in recognition memory for faces with different emotional expressions (neutral, happy, and angry). Subjects slept or remained awake in an 8-h consolidation period in the night following learning, and memory performance was tested two days later. The principal finding is that recognition memory for the faces was enhanced when sleep rather than wakefulness followed learning, and that this effect did not depend on facial expression. The sleep effect was observed selectively for the measure of memory accuracy, i.e. the difference between hit rate and false alarm rate, rather than for hit rates or false alarm rates per se. This pattern indicates an effect of sleep vs. wakefulness on memory performance independent of the individual response criterion at recognition testing, which is confirmed by the fact that the response bias in recognition memory did not differ significantly between the two conditions.

The beneficial effect of sleep vs. wakefulness on face memory cannot be attributed to unspecific effects resulting from prolonged sleep deprivation in the wake condition, because recognition memory was tested after a delay of two days, which included a recovery night at home (monitored by actimetry). Subjective ratings of sleepiness, activation, motivation, boredom, concentration, and tension obtained at learning and recognition testing confirmed the effectiveness of this procedure. None of these measures was differentially affected by sleep and wake conditions. On the whole, subjects even felt less sleepy and more activated at recognition testing than at learning, which further supports the effectiveness of the recovery night spent at home in re-establishing cognitive functioning after a night of sleep deprivation.

Our finding of a facilitating effect of sleep on recognition memory for faces adds to previous research in humans and animals indicating a critical function of sleep for the consolidation of memories, as demonstrated for different explicit and implicit memory tasks in other domains (Fowler et al., 1973; Gais, Plihal, Wagner, & Born, 2000; Maquet, 2001; Stickgold, Whidbee, Schirmer, Patel, & Hobson, 2000b; Stickgold, 2005; Wagner et al., 2004). Showing a supporting effect of sleep also in an explicit face memory task, our results underline the ubiquitous nature of the phenomenon. Face recognition, although relying on domain-specific processing in distinct brain systems (Allison et al., 1994; Farah, 1996; Kanwisher, 2000; Tsao et al., 2006), nevertheless appears to be subject to the more general mechanisms underlying sleep-associated memory consolidation. It is to be noted, however, that the present study does not allow any direct conclusions with respect to these underlying mechanisms. The majority of recent studies in animals and humans has favored the view that sleep supports memory consolidation through an active process presumably involving a covert reactivation of recently acquired memory representations during sleep, and the present study was also designed from this perspective (e.g., Born, Rasch, & Gais, 2006; Buzsáki, 1998; Gais & Born, 2004a; Pennartz et al., 2002; Wilson & McNaughton, 1994). However, other authors have doubted this view (Siegel, 2001; Vertes, 2004). In fact, active consolidation during sleep is not the only possible explanation for memory enhancement after sleep compared to wakefulness. From the beginning of this direction in sleep research, reduced interference during sleep has been proposed as another explanation for improved consolidation of memories or reduced forgetting during post-learning retention periods of sleep in comparison with wakefulness (Jenkins & Dallenbach, 1924; see also Wixted, 2004, for a recent account of this perspective). Our present data are generally consistent with either view and therefore do not contribute to solving this more fundamental issue of the mechanisms of sleep-associated consolidation, which remain to be specified in future studies.

Here, we found a memory-enhancing effect of post-learning sleep vs. wakefulness even with a delay of two days, i.e., some sleep between learning and memory testing also occurred in the wake condition, namely in the second night after learning (the recovery night). Very short sleep periods that are not detectable by actigraphy might have also occurred during daytime in the sleep-deprived waking subjects. Such sleep periods during memory retention in the wake condition, attenuating the experimental sleep effect, may explain why the overall sleep effect in recognition memory here was of moderate size and significant only as a main effect collapsing data from all valence conditions. However, the fact that overall memory performance differed between sleep and wake conditions even despite these attenuating influences further underscores the importance of sleep occurring in a narrow time window after learning for effective consolidation of the newly established memory traces. Previous studies in animals and humans have demonstrated that the sleep period directly following learning is the most critical one for retention of memories even over extended time intervals, although subsequent sleep periods can also support the consolidation process to some degree (Fischer, Hallschmid, Elsner, & Born, 2002; Palchykova, Winsky-Sommerer, Meerlo, Durr, & Tobler, 2006; Smith, Conway, & Rose, 1998; Stickgold, James, & Hobson, 2000a; Wagner, Hallschmid, Rasch, & Born, 2006).

Regarding emotional valence of facial expression, overall recognition memory performance did not differ between emotionally valenced (angry and happy) and neutral faces, which contrasts with the typical finding of emotional enhancement in explicit memory tasks, i.e. enhanced memory for emotionally valenced (negative and positive) compared to neutral material (Cahill & McGaugh, 1998; Dolan, 2002; Hamann, 2001). One possible reason for our divergent finding is that the emotional stimuli used here (angry and happy faces) had only relatively moderate emotional impact in comparison to stimuli used in previous studies (mostly highly emotional pictures from the International Affective Picture System [IAPS; Lang, Öhman, & Vaitl, 1988], which includes depictions of bloody mutilations, accidents, and physical attacks). This is confirmed by the fact that at learning many of our emotional faces of the "angry" category (although not of the "happy" category) were judged by the subjects as being neutral. This led us to perform an additional analysis, where valence categories were formed on the basis of *individual* valence judgments rather than a priori classification. This analysis, however, likewise failed to reveal any significant effect of valence on memory performance. On the whole, in conjunction with previous studies, these negative findings support the notion that emotional enhancement effects on recognition memory are less consistent than on free recall measures typically used in such experiments (Dolan, 2002; Johansson et al., 2004).

Several studies in fact indicated that emotional valence affects recognition memory primarily by changing the response criterion, as expressed in a more liberal response bias for emotional as compared to neutral items, but not by enhancing memory per se (Johansson et al., 2004; Joyce & Kutas, 2005; Windmann & Kutas, 2001). Here, we did not find such an emotion-related response bias. One reason may be again the comparably low emotional impact of our stimuli. Another factor could be the relatively long time delay of two days between learning and recognition testing. It has been shown that subjects respond more conservatively in recognition tests after long compared to short retention intervals (Joyce & Kutas, 2005), an effect that would counteract liberal response bias for emotional stimuli particularly in conditions of delayed recognition testing as applied here.

Response times in the recognition task were overall in the same order of magnitude as reported previously for similar tasks of face recognition memory (e.g., Henson, Shallice, Gorno-Tempini, & Dolan, 2002; Johansson et al., 2004). However, they displayed considerable variability, possibly as a result of the relatively long delay between learning and recognition testing in the present study. An increased impact of individual differences in response strategies enhancing the variance in response time, should be expected particularly after extended retention intervals, when subjects are likely to feel less confident in their judgments than shortly after learning. This variability may have prevented here the revelation of an overall faster reaction to old than new faces (i.e. repetition priming as an indicator for implicit face memory; see Ellis, Young, Flude, & Hay, 1987; Gabrieli, 1998; Squire, 1992), as well as an impact of sleep on this effect (Wagner et al., 2003). Electrophysiological rather than reaction time measures may turn out to be more sensitive to reveal effects of sleep on unconscious aspects of memory processing after extended time delays, as has been shown also for other tasks (Atienza, Cantero, & Stickgold, 2004; Joyce & Kutas, 2005).

Although our study was not primarily designed to reveal effects of specific sleep stages on memory formation for faces, additional exploratory correlation analyses provided several hints in this regard. The amount of NonREM sleep (and of total sleep time), but not REM sleep, during consolidation sleep correlated positively with memory accuracy for the faces at recognition testing. These correlations perfectly replicate results from Clemens et al. (2005), who likewise found in a face memory task a significant relationship between the amount of NonREM sleep as well as total sleep time in the night after learning and subsequent recognition memory performance for the learned faces. Together with findings from other studies using non-facial stimuli in explicit memory tasks, this supports the general notion of a decisive role for NonREM sleep rather than REM sleep in the formation of explicit memories (Fowler et al., 1973; Gais & Born, 2004a; Plihal & Born, 1997, 1999; Tucker et al., 2006), although most of those previous studies more specifically implicated SWS rather than overall NonREM sleep in memory consolidation in their tasks. Both the present study and the study by Clemens and colleagues (2005), as the only sleep studies that used facial stimuli in explicit memory tasks so far, did not find a significant correlation between SWS alone and memory for faces, suggesting that the specific influence of SWS on explicit memory is material-specific and does not apply to tasks using facial stimuli. Even with non-facial material, however, it is still a matter of debate which specific feature of sleep underlies the sleep effect on memory formation in explicit tasks. At least for verbal tasks, recent studies have suggested a critical role for certain processes that are common to both SWS and stage 2 sleep of NonREM sleep, such as sleep spindle activity, slow oscillations, or a downregulation of central nervous cholinergic activity (Gais & Born, 2004b; Marshall, Helgadottir, Mölle, & Born, 2006; Rasch, Born, & Gais, 2006; Schabus et al., 2004). On the other hand, when highly emotional rather than neutral verbal material is used in explicit tasks, REM sleep appears to contribute decisively to memory consolidation (Wagner et al., 2001). Here, REM sleep was not significantly correlated with any measure of explicit face memory, regardless of facial expression. However, REM sleep was strongly associated with a speeding of correct responses for old faces as well as with the difference in reaction times between old and new faces, i.e. repetition priming reflecting implicit memory for the learned faces (Ellis et al., 1987; Gabrieli, 1998; Squire, 1992), which is consistent with our previous findings indicating a beneficial role of REM sleep in repetition priming for facial stimuli (Wagner et al., 2003). In conjunction with a broad variety of studies using different types of other implicit memory tasks, these results support the notion that REM sleep is generally implicated in implicit aspects of memory processing (e.g., Karni et al., 1994; Maquet, 2001; Peigneux et al., 2003; Plihal & Born, 1997, 1999), although these aspects were not critical for retrieval performance in our task since reaction time measures remained overall unchanged by sleep. Thus, although the results of our correlation analyses must generally be interpreted with caution because of possible type I errors due to the great number of correlations performed, they overall fit well with previous findings, likewise suggesting differential functions of NonREM vs. REM sleep in memory formation.

The fact that we measured reaction times in a task that required subjects to indicate by conscious decision whether the stimuli were known or unknown to them raises the question to what degree repetition priming here actually reflects implicit memory. Although in research of repetition priming of faces assessment of priming within a known/unknown decision task is a relatively common procedure (e.g., Ellis et al., 1987, Ellis, Flude, Young, & Burton, 1996), explicit aspects of memory could "contaminate" the implicit memory measure in such tasks. However, there is evidence that when speeded responding is required (as was the case here), such contamination is minimal because the decision is then primarily a result of fast automatic processes that are based on an immediate feeling of familiarity rather than on a recollective memory search (Horton, Wilson, & Evans, 2001; Yonelinas & Jacoby, 1994). To test the relationship between explicit and implicit memory performance in our task directly, we correlated memory accuracy (reflecting explicit memory) in the recognition test with the implicit memory measure of Old-New differences in reaction times across subjects. There was no substantial association between the two measures ($r = -.31$, $p = .32$), indicating that they indeed reflect basically different memory processes. The same result was obtained when we considered separately the old faces (correlation between the number of hits and reaction times for hits: $r = -.13$, $p = .68$), or the new faces (correlation between the number of correct rejections and reaction times for correct rejections: $r = -.34$, $p = .27$). This statistical independence of the explicit and implicit memory measures also indicates that there was no substantial speed-accuracy trade-off. Although a certain degree of mutual influences still cannot be excluded, these analyses indeed support the notion that our reaction time measures of implicit memory assessed processes essentially different from those underlying explicit memory performance, and that implicit and explicit memory measures were not changed at the expense of each other.

In conclusion, we found a beneficial effect of post-learning sleep vs. wakefulness on explicit memory for faces in a recognition memory task. Whereas the effect was independent of emotional valence of facial expression here, valence effects may be revealed with stronger emotional expressions than those used here, e.g. crying rather than angry faces, and laughing rather than smiling faces. Our additional correlation analyses suggest that NonREM sleep and REM sleep affect different aspects of recognition memory for faces, with NonREM sleep playing the primary role for maintaining an explicitly accessible memory trace for the previously encountered faces, while REM sleep seems to support face recognition implicitly by speeding responses to known as compared to unknown faces.

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