Dissociating the contributions of slow-wave sleep and rapid eye movement sleep to emotional item and source memory

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A B S T R A C T

Sleep benefits the consolidation of emotional memories, and this influence is commonly attributed to the rapid eye movement (REM) stage of sleep. However, the contributions of sleep stages to memory for an emotional episode may differ for the event per se (i.e., item memory), and the context in which it occurred (source memory). Here, we examined the effects of slow wave sleep (SWS) and REM sleep on the consolidation of emotionally negative and neutral item (picture recognition) and source memory (recall of picture-location and picture-frame color association) in humans. In Study 1, the participants (n = 18) learned 48 negative and 48 neutral pictures which were presented at specific locations and preceded by colored frames that had to be associated with the picture. In a within-subject design, learning was either followed by a 3-h early-night SWS-rich or by a late-night REM sleep-rich retention interval, then retrieval was tested. Only after REM-rich sleep, and not after SWS-rich sleep, was there a significant emotional enhancement, i.e., a significantly superior retention of emotional over neutral pictures. On the other hand, after SWS-rich sleep the retention of picture-frame color associations was better than after REM-rich sleep. However, this benefit was observed only for neutral pictures; and it was completely absent for the emotional pictures. To examine whether this absent benefit reflected a suppressive effect of emotionality on associations of minor task relevance, in Study 2 we manipulated the relevance of the picture-frame color association by combining it with information about monetary reward, following otherwise comparable procedures. Here, rewarded picture-frame color associations were equally well retained over SWS-rich early sleep no matter if the frames were associated with emotional or neutral pictures. Results are consistent with the view that REM sleep favors the emotional enhancement of item memory whereas SWS appears to contribute primarily to the consolidation of context-color information associated with the item.

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1. Introduction

Emotional memories are remembered better than neutral memories (LaBar & Cabeza, 2006; McGaugh, 2000) and there is also a preferential consolidation of emotional over neutral memory during sleep (Payne & Kensinger, 2011; Van der Helm & Walker, 2009; Wagner, Hallschmid, Rasch, & Born, 2006). This memory benefit for emotional relative to neutral content has been termed "emotional enhancement" and is used here – as in previous studies – as a measure to specifically define emotional memory (LaBar & Cabeza, 2006; Payne & Kensinger, 2011; Wagner, Gais, & Born, 2001). The emotion-induced improvement of long-term memory has been

linked to increased amygdala and parahippocampal activation present during encoding as well as during rapid eye movement (REM) sleep (Kensinger & Schacter, 2006; Maquet et al., 1996; Miyauchi, Misaki, Kan, Fukunaga, & Koike, 2009; Nofzinger, Mintun, Wiseman, Kupfer, & Moore, 1997), in addition to qualitative changes in the emotional memory retrieval network after sleep (Payne & Kensinger, 2011). Studies, which have mostly examined recognition-based item memory, revealed that EEG theta activity (4–8 Hz) during REM sleep correlates with emotional memory gains after sleep (Hu, Stylos-Allan, & Walker, 2006; Nishida, Pearsall, Buckner, & Walker, 2009; Popa, Duvarci, Popescu, Léna, & Paré, 2010). Studies using a split-night design demonstrated an emotional enhancement effect, i.e. a superior free recall of emotional compared to neutral text materials, specifically after a 3-h post-learning interval during the late night filled with

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REM-rich sleep, but not after an early-night period of sleep rich in slow wave-sleep (SWS) or after retention intervals of wakefulness (Groch, Wilhelm, Diekelmann, & Born, 2013; Wagner et al., 2001). Thus, REM sleep seems to play a role in emotional memory formation leading to better retention of emotional as compared to neutral content.

Emotional arousal can increase both memory of the object itself, i.e., familiarity-based item memory, as well as memory of the spatiotemporal context the object is presented in, i.e., source memory (Mather & Nesmith, 2008; McIntyre, Power, Roozendaal, & McGaugh, 2003). However, with regard to source memory, there is also notable evidence that an effect in the opposite direction can occur under specific conditions commonly known as weapon focus, i.e., for an arousal-induced inhibition of contextual memory formation (Loftus, Loftus, & Messo, 1987; Mather, 2007; Steblay, 1992). Here, a central emotional object in the foreground of a scene is preferentially remembered at the expense of peripheral background information, reflecting an emotion-induced impairment of contextual binding. The selective consolidation of emotional item over neutral associated source information is promoted by sleep (Payne, Chambers, & Kensinger, 2012; Payne, Stickgold, Swanberg, & Kensinger, 2008; see e.g., Lewis, Cairney, Manning, & Critchley, 2011, for findings that, the other way around, emotional context information does not seem to selectively influence sleep-related consolidation of associated neutral items). However, the specific contributions of sleep stages to this process remain enigmatic. Indeed, selectivity in sleep-dependent consolidation based on the criterion of future relevance of information (rather than emotionality) has been linked to SWS rather than REM sleep-related memory processing (Diekelmann & Born, 2010; Bendor & Wilson, 2012; Wilhelm et al., 2011). There are also hints that SWS is involved in the strengthening of contextual source information for both neutral materials (Drosopoulos, Wagner, & Born, 2005; Drosopoulos, Windau, Wagner, & Born, 2007; Wilhelm, Wagner, & Born, 2011) as well as for emotional materials (Groch et al., 2011).

Here, we aimed to dissect the roles of REM sleep and SWS in memory consolidation of emotional and neutral items, i.e., the pictures, and their associated context information, i.e., specifically the location of the picture on a computer screen and the color of a frame that preceded the presentation of the picture. We hypothesized that REM sleep supports emotional enhancement of item memory and SWS consolidates associated source information. Study 2 set out to further explore whether effects of sleep stages on the consolidation of context-color information depend on the relevance of the picture-context association. To this end, the presentation of the colored frame preceding the picture was combined with information about a monetary reward that would be received for later correct recall of the picture-frame-color associations, making the frame-color more salient and immediately task relevant.

2. Methods

2.1. Participants

Two studies were conducted, with 18 participants (mean age: 21.27 yrs, range 18–26 yrs; 12 women) taking part in the main experiment (Study 1) and 18 different participants (22.11 yrs, range 19–25 yrs, 10 women) taking part in an additional experiment (Study 2). Participants were native German speakers, non-smokers, free of medication, had no history of neurological, psychiatric or endocrine disorders, and followed a normal sleep-wake rhythm (i.e., no shift work, usual sleep time 2300–0700 h) for at least four weeks before the experiments. Prior to the experiments, subjects were accustomed to sleeping under laboratory

conditions during an adaptation night, including attachment of electrodes for polysomnographic recordings. On experimental days they were required to get up at 0700 h and not to consume caffeine or alcohol. The study was approved by the ethics committee of the University of Luebeck and all participants gave written informed consent prior to participation.

2.2. Design and procedure

Fig. 1A illustrates the design of Study 1. The study was conducted according to a within-subject cross-over design with the order of conditions ("early sleep" vs. "late sleep") balanced across participants, and an interval of at least two weeks between the participant's two conditions. Participants reported to the lab at 2100 h for the early night condition and at 2200 h for the late night condition. Each condition started with the attachment of electrodes. For the early sleep condition, participants learned the task between 2200 and 2240 h (learning phase). This "learning phase" included an immediate (baseline) recall test 5 min after the learning proper. A 3-h retention period of sleep followed (lights off 2300 h), which was expected to be rich in SWS. Thereafter, in the retrieval phase (0300–0340 h), delayed task recall was tested. In the late sleep condition, participants first slept for about 3 h (starting 2300 h) before the learning phase (0300–0340 h) took place (with the learning phase again including an immediate recall test 5 min after learning). Then, a 3-h retention interval of REM sleep-dominated sleep followed (lights off 0400 h). The retrieval phase took place between 0800 and 0840 h.

Thus, the retention intervals in the two experimental conditions were characterized by either high amounts of SWS (early sleep) or high amounts of REM sleep (late sleep), with the start of the 3-h period being determined by sleep onset. After 3 h, participants were awakened as soon as they entered sleep stage 1 or 2 and subsequent testing was timed 45 min later to allow the participant to recover from sleep inertia. Awakenings from SWS and REM sleep were avoided to exclude confounding effects on memory performance by prolonged sleep inertia (e.g., Stones, 1977). Before each learning phase subjects indicated their level of sleepiness on a scale from 1 (active, alert) to 7 (very sleepy) (Stanford Sleepiness Scale, SSS; Hoddes, Dement, & Zarcone, 1972) and performed a 5-min version of the Psychomotor Vigilance Test (PVT; Roach, Dawson, & Lamond, 2006). Also the day's mood was assessed using the Positive And Negative Affect Scale (PANAS, Watson, Clark, & Tellegen, 1988).

Study 2 followed the same procedure. However, it focussed on the early SWS-rich sleep interval only.

2.3. Memory task

2.3.1. Materials

For the picture learning task, four-hundred pictures were selected from the International Affective Picture System (IAPS; Lang, Greenwald, Bradley, & Hamm, 1993) and divided into two parallel sets of 48 low arousing neutral and 48 medium to high arousing negative pictures (for the subjects' two conditions), respectively. To enable two recall tests, i.e., immediate recall testing (baseline) during the learning phase and delayed recall testing during the retrieval phase, each of these sets was again subdivided into two parallel sets each containing 24 neutral and 24 emotional pictures; and these sets were each supplemented with 24 new pictures. Normative valence (scale from negative [1], neutral [5] to positive [9]) and arousal (scale from not arousing at all [1] to very arousing [9]) ratings were comparable for the eight sets (all $p > 0.99$): [mean ± SD across all sets] valence ratings: negative, 3.11 ± 1.60; neutral, 5.01 ± 1.22; arousal ratings: negative,
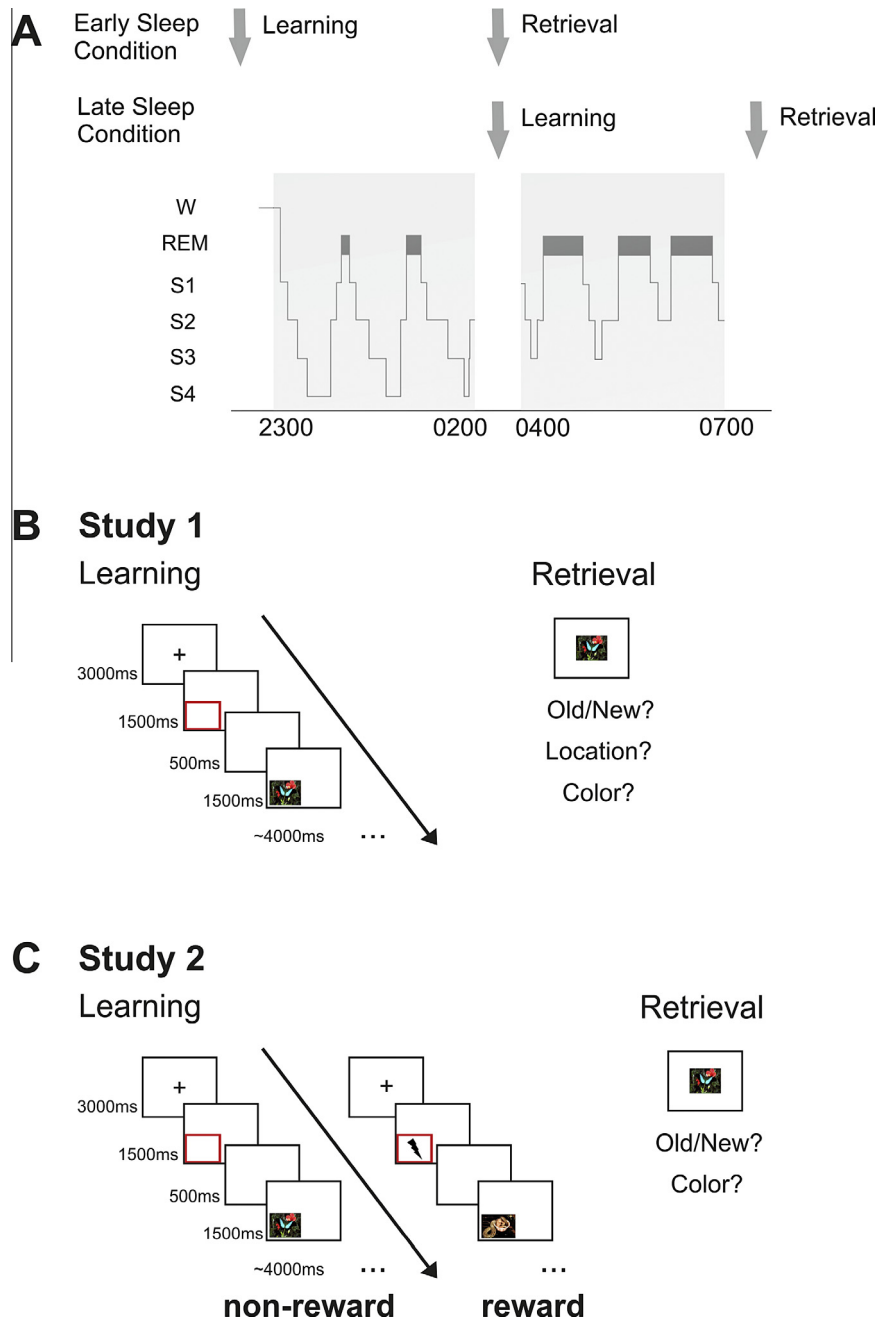
Fig. 1. Design and task of Studies 1 and 2. (A) In Study 1, participants were tested in two conditions (early sleep vs. late sleep). In the early sleep condition, the learning phase (including immediate recall testing) took place between 2200 and 2240 h. This was followed by retention interval containing 3-h of early nocturnal sleep predominated by SWS (lights off 2300); then the retrieval phase with delayed recall testing followed (between 0300 and 0340 h). In the late sleep condition, participants first slept for 3 h (lights off at 2300 h) before the learning phase (between 0300 and 0340 h). Then the retention interval containing 3-h of late REM sleep-dominated sleep (lights off 0400 h) followed before the retrieval phase followed between 0800 and 0840 h. A typical polysomnogram visualizes the proportion of sleep stages during the two nocturnal retention periods of sleep (wake (W), non-rapid eye movement (NonREM) sleep stages 1–4 (S1–S4), REM sleep). In Study 2, participants were tested following the early sleep condition schedule of Study 1. (B) Task in Study 1: The learning task included emotional and neutral pictures. A task trial (picture presentation) started with presentation of a fixation cross, followed by a frame in one of four colors (blue, green, red, or yellow) followed by the presentation of the picture at one of four locations (quadrants of the screen). Inter-trial interval was variable. For retrieval testing, recognition of pictures (presented in the center of the screen) was assessed by old/new judgements and – if a picture was recognized as "old" – the participant had to indicate the location as well as the color of the associated frame for this picture by respective button presses (one out of four buttons). (C) In Study 2, the same picture sets and learning procedures were used except that participants were instructed to only learn the pictures and the picture-frame color associations. Additionally, half of the neutral and negative picture trials were marked by a lightening symbol which was presented simultaneously with the frame and signalled to the participant that, for these stimuli, they would receive a monetary reward if they remembered the respective picture-frame color associations correctly at the later retrieval testing. At retrieval testing, recognition of pictures was assessed by old/new judgements and – if a picture was recognized as old – the participant had to indicate the frame color for this picture by a corresponding button press. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

5.81 ± 2.147; neutral, 3.17 ± 1.92). The stimulus sets were counterbalanced across the sleep conditions.

2.3.2. Learning and recall testings

During learning, pictures were presented in pseudorandomized order following predefined criteria (a maximum of two subsequent pictures with the same valence, each half-set of pictures with an equal amount of emotional and neutral pictures, balanced number of pictures paired with 1 of 4 color frames appearing at 1 of 4 locations), with all participants in both conditions receiving the same order. Each trial (picture presentation, Fig. 1B) started with a fixation cross presented for 3000 ms, followed by a colored (blue, green, red or yellow) frame (1500 ms) and an empty screen (500 ms). The picture (500 × 364 pixels, i.e., sized 18 × 13 cm on the screen) was presented for 1500 ms at one of four locations (left or right, top or bottom quadrants). The inter-trial-interval was variable (3500, 4000 or 4500 ms; mean: 4000 ms). Participants were instructed to memorize the pictures, as well as their location and the color of the preceding frame because memory for all these information would be tested later. To accustom participants to the learning procedure and to prevent primacy and recency effects in memory performance, four additional pictures were presented before and after each target picture set which were not included in the analyses. These buffer pictures consisted of two negative and two neutral pictures which were each presented in a different location and preceded by a frame of different color.

Following a 5-min break after learning, immediate recall performance (baseline) for picture recognition was tested by presenting half of the 96 pictures used during learning ('old' pictures) randomly intermixed with 48 new pictures. Each picture appeared in the middle of the screen in pseudorandomized order with the same criteria as during learning. Participants had to indicate with a corresponding key press whether they had seen the picture before ('old') or not ('new'). Only, if participants signalled an "old" picture, they additionally had to indicate the location the picture had appeared in as well as the color of the preceding frame. There was no time limit for responses at recall testing. Delayed recall testing in the retrieval phase after the retention interval was performed for the other half of the 96 pictures used during learning, and followed the same procedure as immediate recall testing at the end of the learning phase.

In Study 2, the task was the same except that participants were instructed to only remember the pictures and the associated frame colors. Additionally, half of the colored frames preceding each picture were marked by a "lightening" symbol in the middle of the frame signalling to the subject that, for this trial, they would receive a monetary reward (50 cents) for later correct recall of the frame-color-picture association (Fig. 1C). This information was added to the stimulus configuration of the frame in order to increase the task relevance of the frame-color itself.

2.4. Sleep recordings

For standard polysomnography, the electroencephalographic (EEG) activity was continuously recorded with (Ag/AgCl) electrodes from C3 and C4 referenced to linked electrodes attached to the mastoids. Additionally, horizontal and vertical electrooculographic (EOG) and electromyographic activity (EMG) were recorded. Data were amplified by BrainAmp Amplifiers (Brain Products GmbH, Gilching, Germany) and continuously digitized at a rate of 250 Hz. Sleep recordings were scored offline according to standardized criteria (Rechtschaffen & Kales, 1968). For each 3-h sleep interval, sleep onset was determined by the first occurrence of stage 1 sleep followed by stage 2 sleep (with reference to light off). Moreover, total sleep time (TST, in min) and the time spent in the different sleep stages (wake; sleep stages 1, 2, 3, 4; SWS,

i.e., sum of sleep stage 3 and 4; REM sleep; in min and in percent of TST) was calculated.

2.5. Data reduction and statistical analysis

For immediate and delayed recall, individual recognition indexes were determined which correct performance for response bias (P_r = hits − false alarms). This corrected index is preferred because false alarm rates are known to be higher for emotional pictures compared to neutral pictures, which was also true for the current study. Then, retention of pictures was quantified as the percent of recognized pictures during the retrieval phase, relative to immediate recall performance at the end of the learning phase (set to 100%). This was done separately for negative and neutral pictures and, in Study 2, also separately for the rewarded and non-rewarded frame-picture associations. (In Study 2, false alarms could not be specifically allocated to either the reward or non-reward category, because false alarms refer to new pictures – falsely recognized as old – which were never actually associated with reward or non-reward. For this reason, in Study 2 half of the false alarms were allocated to the reward and non-reward categories, respectively.) Additionally, we present separate analyses of immediate recall performance at the end of the learning phase and – if effects on the retention measure are significant or approaching significance – the delayed recall performance at retrieval testing, mainly to trace possible confounding influences associated with the circadian phase that differed between the early and late sleep retention conditions.

Similarly, retention of picture-frame color associations and picture locations was calculated as percent values with the number of correctly recalled picture-frame color associations and picture locations at immediate recall testing set to 100%. Because in Study 2 the number of correctly recalled picture-frame color associations per emotion/reward category was small (i.e., below 12) we here additionally performed the analyses with absolute difference measures (delayed recall during retrieval phase minus immediate recall performance during learning phase). These analyses lead to essentially the same results.

Statistical data analysis was based on Analyses of Variance (ANOVA) with the repeated measures factors 'emotionality' (negative/neutral) and 'early/late sleep' in Study 1 and, additionally, 'rewarded/non-rewarded' in Study 2 for analyses of retention scores as well as separate assessment of recall performance during learning and retrieval phases. Significant ANOVA effects were followed by post hoc t-tests. The level of significance was set to $p = .05$ and Greenhouse–Geisser correction was applied when appropriate.

3. Results

3.1. Study 1

3.1.1. Recognition of pictures

Consistent with our hypothesis, retention of pictures (i.e., the percent recognition index with performance at immediate recall set to 100%) revealed superior retention for negative over neutral pictures only after the late REM sleep-rich retention interval ($p = .02$) whereas no such difference was detected after early SWS-rich sleep ($p = .12$), with the respective early/late sleep × emotionality interaction approaching significance ($F(1,17) = 3.36$, $p = .08$, Fig. 2A). Concentrating on picture recognition performance during the retrieval phase confirmed this pattern with a distinctly enhanced recognition of emotional over neutral pictures only after REM-rich late sleep ($p = .04$) but not after SWS-rich early sleep ($p = .45$; $F(1,17) = 5.02$, $p = .04$, for early/late
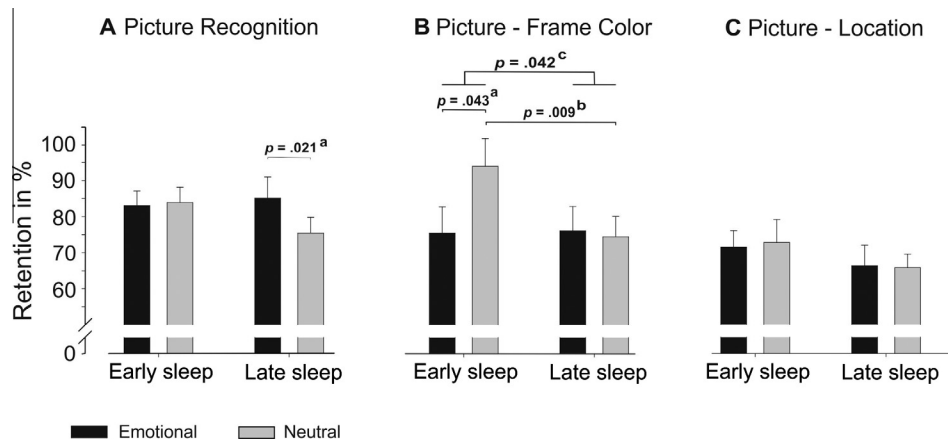
Fig. 2. Retention across early and late sleep intervals in Study 1, assessed for (A) picture recognition, and (B) recall of picture-frame color associations and (C) of picture locations. Retention of pictures (recognition at retrieval relative to performance at immediate recall at the end of the learning phase) was superior for emotional over neutral item only across late REM-rich sleep but not across early SWS-rich retention sleep. In contrast, picture-frame color associations were retained better across early SWS-rich than across late REM-rich sleep. However, this effect was specific to neutral pictures and entirely absent for the emotional pictures. Memory for picture locations was not differentially affected by early or late retention sleep. P-values for post hoc pairwise comparisons are indicated ([a]comparison between emotional and neutral items per sleep condition; [b]comparison between early and late sleep condition for neutral items; [c]ANOVA interaction effect early/late sleep × emotional/neutral).

sleep × emotionality interaction). Recognition performance at the end of the learning phase (immediate recall) was generally high and neither differed between early vs. late sleep conditions, nor for emotional vs. neutral pictures ($p > .14$ for respective main and interaction effects; see Table 1 for a summary of recognition data).

3.1.2. Recall of picture-frame color associations and picture locations

Note that the number of pictures (items) correctly recognized determined the maximum of associated frame colors and positions (source) that could be correctly retained. As for picture recognition, to determine retention of associated frame colors and picture positions, performance in the retrieval phase was related to (immediate recall) performance during the learning phase (set to 100%). Retention of picture-frame color associations tended to be better across early than late sleep ($F(1,17) = 3.27$, $p = .09$ for the main effect of early/late sleep), however only for the neutral pictures ($p = .01$). For the emotional pictures this difference was entirely absent ($p = .93$, $F(1,17) = 4.85$, $p = .04$, for early/late sleep × emotionality, Fig. 2B). Indeed, pairwise comparisons for the early sleep condition showed that retention of picture-frame color association

for emotional pictures was even significantly worse than that for neutral items ($p = .04$). This pattern was paralleled in the absolute performance scores at delayed recall: most importantly, the interaction early/late sleep × emotionality was again significant ($F(1,17) = 4.46$, $p = .05$). Retention of picture locations was neither differentially affected by the emotionality of the pictures nor the early and late retention sleep condition ($p > .34$, for the respective main and interaction effects, Fig. 2C).

At immediate recall at the end of the learning phase, the number of recalled picture-frame color associations was comparable between the early and late sleep conditions ($p > .17$, for respective main and interaction effects). Recall of picture-frame color associations was generally better for neutral compared to emotional pictures ($p = .02$ for the main effect of emotionality). Immediate recall of picture locations was generally better before early than late retention sleep ($p = .03$), but not significantly different for emotional and neutral pictures ($p = .55$). To rule out a possible confounding factor such that subjects associated a frame color with the preceding rather than the succeeding picture an exploratory error analysis was conducted. This inspection did not provide any

Table 1
Study 1: Picture recognition and recall of picture-frame color associations and picture locations.

		Early sleep		Late sleep	
		Emotional Mean ± SEM	Neutral Mean ± SEM	Emotional Mean ± SEM	Neutral Mean ± SEM
Picture recognition					
Hits – FA	Learning	20.50 ± 0.8	21.33 ± 0.5	20.22 ± 0.7	20.28 ± 0.8
	Retrieval	17.17 ± 1.0	17.89 ± 1.0	17.28 ± 1.2	15.56 ± 1.2[a,b]
	Retention (in %)	83.06 ± 4.1	83.88 ± 4.3	85.08 ± 5.9	75.42 ± 4.4[a,b]
Picture-frame color association					
Hits	Learning	11.94 ± 1.1	13.22 ± 1.3	10.67 ± 0.9	12.17 ± 1.1
	Retrieval	8.94 ± 1.1	11.72 ± 1.2[a]	8.00 ± 1.0	9.17 ± 1.1[b]
	Retention (in %)	75.46 ± 7.3	94.04 ± 7.8[a]	76.09 ± 6.8	74.48 ± 5.7[b]
Picture location					
Hits	Learning	13.89 ± 0.9	14.17 ± 1.1	12.94 ± 0.9	12.67 ± 1.1[b]
	Retrieval	10.11 ± 1.0	10.00 ± 1.0	8.50 ± 0.9[b]	8.44 ± 0.9
	Retention (in %)	71.53 ± 4.5	72.75 ± 6.4	66.33 ± 5.7	65.78 ± 3.7

Memory performance is indicated at the end of the learning phase (immediate recall) and at the retrieval phase (delayed recall) for picture recognition by the mean ± SEM number of recognized items (Hits) minus false alarms (FA), as well as for recall of picture-frame color associations and picture locations by the mean ± SEM number of hits. Additionally, retention is indicated as percent values of recall performance at delayed recall with performance at immediate recall set to 100%. Values are indicated separately for the early and late sleep condition and for emotional and neutral pictures. Post hoc pairwise comparisons are presented for learning, retrieval, and retention for completeness.
[a] $p < .05$, for pairwise comparisons between emotional and neutral pictures within each sleep condition.
[b] $p < .05$, for pairwise comparisons between early and late sleep conditions for emotional and neutral pictures.

hint that subjects tended to form these erroneous associations: the frequency of such errors was only negligibly different from chance level.

3.1.3. Sleep

Analyses of sleep data confirmed the expected prevalence of SWS in the early sleep condition and of REM sleep in the late sleep condition for each participant ([mean ± SEM] SWS; early sleep: 38.26 ± 4.08%, late sleep: 12.24 ± 1.98%; REM; early sleep: 8.54 ± 1.37%, late sleep: 29.14 ± 1.56%; both $p < .001$). None of the other sleep stages differed between conditions (see Table 2 for a summary of the sleep results). On an exploratory basis, correlations were calculated between the time spent in SWS and REM sleep, respectively in the different retention sleep conditions, and the retention measures of interest. However, none of these coefficients reached significance ($p > .05$), possibly due to the fact that the split-night design is constructed in order to decrease across-subject variance in the amounts of SWS and REM sleep, respectively, making it difficult to unmask such correlations.

3.1.4. Sleepiness, vigilance, and mood

Self-reported sleepiness did not differ between conditions at learning (early sleep condition: 3.28 ± 0.30, late sleep condition: 3.83 ± 0.27, $p = .07$). However, participants reported to be less tired at retrieval after late than after early sleep (early sleep: 3.44 ± 0.31, late sleep: 2.72 ± 0.30; $p = .05$). Reaction times on the vigilance task were comparable between sleep conditions at retrieval testing (early sleep: 303.09 ± 6.30 ms vs. late sleep: 307.38 ± 6.90 ms, $p = .39$). However, in the learning phase reaction times were faster in the early than late sleep condition (296.74 ± 6.02 vs. 310.81 ± 6.13, $p = .01$). Mood measures were well comparable between conditions (PANAS – positive affect: early sleep, 25.94 ± 1.97, late sleep, 23.67 ± 1.63; negative affect: early sleep, 11.72 ± 0.44, late sleep, 11.61 ± 0.47; all $p > .17$).

3.2. Study 2

Study 1 revealed that early SWS-rich sleep benefitted the retention of picture-frame color associations as compared to REM-rich sleep. However, unexpectedly, this effect was entirely absent for the emotional pictures. In Study 2, we tested whether such absence of a SWS-related benefit in context-color memory for the emotional pictures reflects an emotion-related suppression of aspects in a memory that are of minor task relevance. For this purpose, in this study half of the neutral and emotional picture trials were directly associated with a monetary reward that could be earned during later correct recall of picture-frame color associations.

3.2.1. Recognition of pictures

Importantly, the comparison of memory measures indicated that retention across early sleep (in percent with respect to immediate recall) was highly comparable between emotional and neutral pictures ($F(1,17) = 0.01$, $p = .92$, main effect emotionality), and this outcome did not depend on whether the trial was rewarded or not ($p > .11$ for the respective main and interaction effects, see Table 3 and Fig. S1 for a summary of recall results). Separate analyses of the immediate recall at the end of the learning phase indicated a reward effect with better recall for rewarded in comparison to non-rewarded pictures ($p = .04$), but no differences between neutral and emotional pictures ($p > .62$, for the respective main and interaction effects).

3.2.2. Recall of picture-frame color associations

Analyses indicated that retention of picture frame color associations (percent values with the number of correctly recalled picture-frame color associations at immediate recall testing set to 100%) across early sleep was highly comparable between emotional and neutral pictures ($F(1,17) = 0.23$, $p = .64$, main effect emotionality), and this outcome did not depend on whether the trial was rewarded or not ($p > .59$ for the respective main and interaction effects). To elaborate on these findings, we compared retention of picture-frame color associations for emotional and neutral pictures across early sleep between Study 2 and Study 1 (taking number of correctly recalled picture-frame color associations at immediate recall as covariates into account). This analysis confirmed that retention of picture-frame color associations was comparable for emotional and neutral pictures in Study 2, whereas picture-frame color associations for the emotional pictures were retained at a distinctly lower level than for the neutral pictures in Study 1 ($F(1,32) = 4.61$, $p = 0.039$, for emotionality × Study 1/2 interaction, Figs. 3 and S1). Immediate recall of picture-frame color associations was better for rewarded compared to non-rewarded items ($p < .001$) and generally better for neutral compared to emotional items ($p = .04$; interaction not significant, $p = .84$).

3.2.3. Sleep, sleepiness, vigilance, and mood

Sleep during the early SWS-rich retention interval was comparable with that in Study 1 (Table 2). Also, sleepiness and vigilance scores in Study 2 were comparable to those of the early sleep condition of Study 1: PANAS – positive affect: 25.22 ± 1.71; negative affect: 12.56 ± 0.73; self-reported sleepiness – at learning: 3.28 ± 0.19; at retrieval: 3.56 ± 0.26; vigilance – at learning: 298.61 ± 6.05 ms; at retrieval: 306.65 ± 7.07.

4. Discussion

The results of our study point towards distinct functions of SWS and REM sleep in emotional memory processing. On the one hand, we found a specific, relative enhancement of emotional compared to neutral picture recognition, only after a period of late REM-rich retention sleep but not after early SWS-rich retention sleep, which corroborates previous studies (Groch et al., 2013; Wagner et al., 2001). Although – due to limitations, such as a missing wake control conditions – our study does not allow for straight forward conclusions as to the specific role of REM sleep, our data appears to be consistent with the view, elaborated in previous studies (e.g., Nishida et al., 2009; Payne et al., 2012), that REM sleep contributes to consolidating emotional item memory. REM sleep has been repeatedly shown to enhance emotionally arousing as compared to neutral item memory (Groch et al., 2013; Nishida et al., 2009;

Table 2
Sleep parameters: Studies 1 and 2.

	Study 1		Study 2
	Early sleep Percentage of TST Mean ± SEM	Late sleep Percentage of TST Mean ± SEM	Early sleep Percentage of TST Mean ± SEM
Sleep parameters			
Wake	0.77 ± 0.25	0.29 ± 0.08	2.78 ± 1.26
Stage 1	7.37 ± 1.18	8.93 ± 0.79	5.74 ± 0.76
Stage 2	44.32 ± 2.96	48.53 ± 1.62	46.98 ± 2.27
Stage 3	21.96 ± 1.97	10.32 ± 1.52**	17.55 ± 1.67
Stage 4	16.31 ± 3.18	1.92 ± 0.97**	18.00 ± 2.64
SWS	38.26 ± 4.08	12.24 ± 1.98**	35.55 ± 2.95
REM	8.54 ± 1.37	29.14 ± 1.56**	8.54 ± 1.12
TST (in min)	186.72 ± 2.21	185.50 ± 1.07	188.92 ± 4.43

Sleep parameters are given in mean (±SEM) of absolute time in minutes and percentage of total sleep time; SWS = slow wave sleep (sum of sleep stages 3 and 4), REM = rapid eye movement sleep, TST = total sleep time; *t*-tests were calculated between the early and late sleep condition in study 1,
** $p < 0.01$.

Table 3
Study 2: Picture recognition and recall of picture-frame color association.

		Rewarded		Non-rewarded	
		Emotional Mean ± SEM	Neutral Mean ± SEM	Emotional Mean ± SEM	Neutral Mean ± SEM
Picture recognition					
Hits – FA/2	Learning	10.56 ± 0.3	10.53 ± 0.4	9.83 ± 0.4	9.53 ± 0.5
	Retrieval	8.89 ± 0.4	9.58 ± 0.4	8.56 ± 0.5	7.36 ± 0.6[a,b]
	Retention (in %)	84.84 ± 3.5	92.84 ± 4.6	88.05 ± 6.0	79.14 ± 6.5
Recall of picture – frame color association					
Hits	Learning	7.94 ± 0.5	8.83 ± 0.6[a]	5.17 ± 0.6[b]	5.89 ± 0.6[b]
	Retrieval	6.33 ± 0.4	7.11 ± 0.5	3.44 ± 0.5[b]	4.11 ± 0.5[b]
	Retention (in %)	81.86 ± 4.6	81.69 ± 4.4	73.85 ± 9.3	81.83 ± 12.1

Memory performance is indicated at the end of the learning phase (immediate recall) and at the retrieval phase (delayed recall) for picture recognition by the mean ± SEM number of recognized items (Hits) minus false alarms (FA/2), as well as for recall of picture-frame color associations by the mean ± SEM number of hits. Additionally, retention is indicated as percent values of recall performance at delayed recall with performance at immediate recall set to 100%. Values are indicated separately for emotional and neutral pictures and separately for rewarded and non-reworded trials. Post hoc pairwise comparisons are presented for learning, retrieval, and retention for completeness.

[a] $p < .05$, for pairwise comparisons between emotional and neutral pictures within each reward condition.
[b] $p < .05$, for pairwise comparisons between rewarded and non-rewarded items for emotional and neutral pictures.
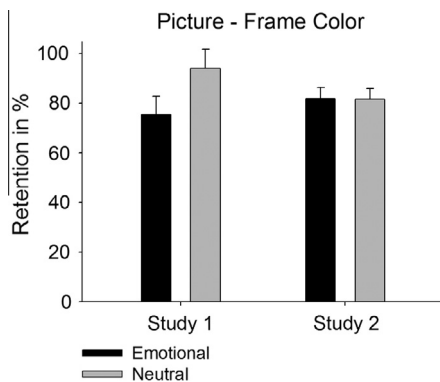

Fig. 3. Retention of picture-frame color associations across the early sleep interval in Study 1 (all pictures) and Study 2 (rewarded pictures only). Picture-frame color associations were retained better for emotional compared to neutral pictures in Study 1, whereas this emotionality difference was completely absent for the retention of rewarded picture-frame color associations in Study 2. Note that direct comparisons of values of retention performance between Study 1 and 2 should be done with caution and take the differences in task procedures into account.

Wagner et al., 2001), an effect possibly related to increased activity of the amygdala and parahippocampal areas during REM sleep (Maquet et al., 1996; Miyauchi et al., 2009; Nofzinger et al., 1997). This view basically assumes that the brain adds strength to a memory for emotional as compared to neutral materials (i.e., the emotional enhancement). However, as the emotional enhancement is defined by the difference in the retention of emotional minus neutral items, the change in this difference could be also interpreted as a change in retention of neutral items. Thus, it could be argued that REM vs. SWS-rich sleep differentially affects the retention of neutral rather than emotional items. Along this line, late REM-rich sleep may specifically act to degrade neutral and irrelevant information (Crick & Mitchison, 1983), leaving emotional memory unaffected. This view seems to also be supported by the fact that in the present study recognition of the emotional pictures was comparable for the early and late sleep condition. Note, however, that retention rates in the late sleep condition tended to be lower in general. Moreover, with the exception of computational models, previous work has provided little support for a specific role of REM sleep in degrading irrelevant and neutral materials (for a summary see e.g., Rasch & Born, 2013). Nevertheless, the specific mechanisms by which REM sleep influences emotional vs. neutral item memory remain elusive and call for further examination.

On the other hand, we found that SWS, relative to REM, enhanced the retention of frame colors associated as a context with the pictures. Interestingly, this enhancing effect of SWS-rich sleep was observed only for neutral pictures, whereas it was completely absent for the emotional pictures. However, retention across SWS-rich early sleep of frame colors for emotional pictures was closely comparable with that for neutral pictures when, in the Supplementary Study 2, information about expected reward for later recall was added to the frame. Thus, our data suggest that SWS supports the retention of some aspects of source memory, although this conclusion is hampered by the fact that our Study 1 did not reveal a clear benefiting effect of SWS-rich early sleep on the retention of the frame locations. That the retention of context-color memory seems to depend on both the task-relevance of source information and the emotionality of the item suggests that SWS is also involved in selecting which information enters sleep-dependent memory consolidation.

The facilitated consolidation of (color-)context information for neutral pictures, specifically during SWS-rich sleep, is in accordance with previous studies that related early night sleep and EEG slow-wave activity hallmarking this period, to hippocampus-dependent source memory consolidation (Binder et al., 2012; Inostroza & Born, 2013; Oyanedel et al., in press; Peigneux et al., 2004; Sterpenich et al., 2007). It also agrees with active system consolidation theory which posits that after encoding, episodic memory binding item and source are temporally stored within hippocampal structures and replayed during SWS. This replay presumably enhances contextually bound episodic representation as well as it promotes a redistribution of the representation towards extrahippocampal networks (Diekelmann & Born, 2010; Inostroza & Born, 2013).

Surprisingly, in our main experiment the context-color enhancing effect of SWS-rich sleep spared emotional pictures. This finding does not only add to growing evidence that beyond REM sleep, SWS essentially contributes to emotional memory processing during sleep (Groch et al., 2011; Hauner, Howard, Zelano, & Gottfried, 2013). It appears to also be closely linked to previous studies showing that nocturnal sleep enhances memory for emotional objects in the foreground of a picture, but concurrently suppresses retention of their neutral peripheral background (Payne et al., 2008, 2012). Our results extend these findings by specifying the sleep stages underlying emotional enhancement in item memory on the one hand and suppressing enhancement of contextual associations on the other. We speculate that during SWS a selection process takes place that decides which source information integrated with an

item will be consolidated during sleep based on the future relevance of this information (Wilhelm et al., 2011).

Indeed, the absent SWS-induced enhancement of picture-frame color associations for emotional items could reflect the much higher attentive value of the emotional item itself overshadowing the participant's intention to associate item and context. This view is corroborated by the main finding of Study 2 indicating comparable retention of associated frame-colors over early sleep intervals for neutral and emotional pictures when the frame simultaneously provided reward information, thus increasing its task relevance. Fittingly, a number of previous studies showed a preferential consolidation of relevant over irrelevant information during sleep, and have also suggested that this selectivity in the sleep-dependent consolidation process is associated with SWS (Fischer & Born, 2009; Van Dongen, Thielen, Takashima, Barth, & Fernández, 2012; Wilhelm et al., 2011). Thus, when the relevance of the association between picture and frame was externally enforced to a comparably strong degree for the emotional and neutral contents, also emotional contextual memory was boosted by SWS-rich early retention sleep. Features like relevance and salience might be a critical factor for modulating the direction of the emotion influence: when emotional objects that are integrated into a relevant context (e.g., a certain cue that predicts the appearance of a threatening emotional stimulus) memory on this context (i.e., the source) is enhanced and conversely, when the context is irrelevant this source information is suppressed. Relevant context information might be tagged during encoding such that it preferentially enters SWS-related processing. This extension of the current view on emotional memory consolidation implicating succeeding roles for SWS in the selection of relevant source memory and for REM sleep in emotional enhancement in item memory is in accordance with the sequential model of memory consolidation sleep, emphasizing the importance of the succession of SWS preceding REM sleep (Ficca & Salzarulo, 2004; Giuditta et al., 1995). Nevertheless, based on the present results this view remains tentative and is in need of confirmation in further studies.

Given that frame relevance countered suppressing effects of item emotionality on memory for associated frame colors in Study 2, one might have expected a boosting effect of subsequent SWS-rich sleep only for frames signalling "reward" but not for the non-reward trials. However, retention of emotional pictures and associated frame colors was not modulated by reward. While unexpected, this outcome suggests that the enhanced relevance of the information associated with the frame per se was the factor tagging for later consolidation, rather than the expected reward. Different from previous studies where differential reward allocations were introduced after the learning phase, here reward information was provided together with the information to be encoded which via a non-specific attention-enhancing influence might tag this information for preferential consolidation during sleep (Benchenane et al., 2010). When comparing findings from Studies 1 and 2 it is important to keep in mind that the two studies did not only differ regarding the reward manipulation that was newly introduced in Study 2. Also, Study 2 did not include the location memory task. This change was introduced to reduce overall cognitive load, and per se might even be responsible for the overall better memory for frame-picture associations in this study. However, in addition, such task modifications likely influence the way the task is processed at learning and the attention allocated to the different aspects of the task configuration. In light of these substantial changes in the task configuration, it might not surprise that certain patterns of results, like the better retention of frame color associations for neutral over emotional pictures in Study 1, did not similarly show up in the non-reward condition of Study 2.

It is also difficult to explain that SWS-rich sleep did not boost retention of picture locations representing source memory as well.

Although previous findings suggest that any kind of contextual binding during encoding, i.e., the location of an object and spatio-temporally separated object associations engages hippocampal activity and should consequently profit from SWS-rich sleep (e.g., Inostroza, Binder, & Born, 2013; Nguyen, Tucker, Stickgold, & Wamsley, 2013; Inostroza & Born, 2013), the extent of hippocampal engagement increases with a greater temporal gap between object and associative feature (Staresina & Davachi, 2009). Against this backdrop it could be argued that location memory presented in different quadrants of the screen is not essentially hippocampus-dependent, making its maintenance independent from sleep (Cansino, Maquet, Dolan, & Rugg, 2002; Sommer, Rose, Gläscher, Wolbers, & Büchel, 2005; Uncapher, Otten, & Rugg, 2006). However, this is a tentative explanation. In addition, baseline difference pointing towards a generally enhanced encoding of picture locations before early retention sleep might have masked any differential effects of early and late retention sleep.

Although the split-night design of the present study is a straight forward approach to compare SWS-rich and REM-rich periods of retention sleep, it bears some limitations. Specifically, although the amount of stage 2 sleep is comparable between early and late-night sleep the quality of the sleep stage, for example, in terms of spindle density may differ across the night (De Gennaro & Ferrara, 2003). Also, memory performance during the late sleep condition could be biased by the fact that subjects slept before the encoding phase of this condition (Yoo, Hu, Gujar, Jolesz, & Walker, 2007). Although we took measures to control for such confounds, e.g., by monitoring vigilance and attention during encoding, they cannot be entirely ruled out. Indeed, as a possible reflection of an influence of circadian rhythmicity, subjects showed slightly slower reaction times before late sleep than before early sleep, and after late sleep felt less tired than after early sleep. Although this observation indicates an obvious limitation of the study, we do not think that these differences in self-rated sleepiness and reaction time can plausibly explain the observed differential effects of REM-rich and SWS-rich retention sleep on emotional enhancement of item memory and context-color memory, respectively. Exploratory analyses did not reveal any significant correlation between reaction times or rated sleepiness and the memory retention measures of interest ($p > .25$). Even more important, except for recall of picture location, baseline measures of immediate recall revealed comparable memory performance for the two retention conditions, making it altogether unlikely that circadian confounds substantially biased the present results.

Acknowledgments

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.nlm.2014.08.013.

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