Brain Research 1698 (2018) 29-42

Contents lists available at ScienceDirect

Brain Research

journal homepage: www.elsevier.com/locate/bres

Research report

Effects of early morning nap sleep on associative memory for neutral and emotional stimuli



Brain Research

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ARTICLE INFO

Article history: Received 15 February 2018 Received in revised form 19 May 2018 Accepted 16 June 2018 Available online 18 June 2018

Keywords: SWS REM sleep Sleep spindles Theta oscillations Item memory Systems consolidation

ABSTRACT

Emotional events are preferentially retained in episodic memory. This effect is commonly attributed to enhanced consolidation and has been linked specifically to rapid eve movement (REM) sleep physiology. While several studies have demonstrated an enhancing effect of REM sleep on emotional item memory, it has not been thoroughly explored whether this effect extends to the retention of associative memory. Moreover, it is unclear how non-rapid eye movement (NREM) sleep contributes to these effects. The present study thus examined associative recognition of emotional and non-emotional material across an early morning nap (N = 23) and sustained wakefulness (N = 23). Nap group subjects demonstrated enhanced post-sleep associative memory performance, which was evident across both valence categories. Subsequent analyses revealed significant correlations between NREM spindle density and presleep memory performance. Moreover, NREM spindle density was positively correlated with post-sleep neutral associative memory performance but not with post-sleep emotional associative memory. Accordingly, only neutral associative memory, but not emotional associative memory, was significantly correlated with spindle density after an additional night of sleep (+24 h). These results illustrate a temporally persistent relationship between spindle density and memory for neutral associations, whereas post-sleep emotional associative memory appears to be disengaged from NREM-sleep-dependent processes.

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1. Introduction

The successful encoding of a specific event merely constitutes the prerequisite to its successful retrieval in the future. Subsequent stages of consolidation are critical for establishing which memory representations will persist over time. Sleep-dependent processes, in particular, are critically involved in memory consolidation, as they enable redistribution of memory representations between different memory subsystems (Diekelmann and Born, 2010; Stickgold and Walker, 2013). Contemporary memory models suggest that sleep-related systems consolidation is largely accomplished during slow wave sleep (SWS). Within this neurophysiological state, previously acquired memory representations are assumed to be gradually redistributed from temporary storage in the hippocampus towards long-term integration into neocortical networks (Diekelmann and Born, 2010). This process is reflected in the temporal synchrony of specific phases of oscillatory features in

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https://doi.org/10.1016/j.brainres.2018.06.020 0006-8993/© 2018 Elsevier B.V. All rights reserved.

the hippocampus (sharp wave ripples), within the thalamocortical circuit (sleep spindles 11-15 Hz) and in the neocortex (slow oscillations <1 Hz). Accumulating evidence indicates that this mechanism may be particularly relevant for the consolidation of hippocampus-dependent associative memory (Mednick et al., 2013; Studte et al., 2015), whereas hippocampus-independent item memory is often retained during wakefulness (van der Helm et al., 2011). The consolidation of memory representations during sleep further relies on learning intention, which is believed to be accomplished by means of top-down-processes. More specifically, prospectively relevant memory representations are assumed to be "tagged" during wakeful encoding (Heib et al., 2015; Marshall and Born, 2007; Rasch and Born, 2013), potentially mediated by the prefrontal cortex (Vorster and Born, 2015). During subsequent SWS, slow oscillations, which are generated in prefrontal regions, are assumed to drive the selective reactivation and reprocessing of these "tagged" memory representations (Born and Wilhelm, 2012). In line with this assumption, stimuli of high future relevance are found to be selectively retained across sleep (Studte et al., 2017; Saletin et al., 2011; Wilhelm et al., 2011; but see Baran et al., 2013;



Tucker et al., 2011), which is accompanied by changes in SWS-related oscillatory features (e.g. sleep spindle density; Saletin et al., 2011; Studte et al., 2017).

Whereas consolidation of neutral material has been primarily linked to SWS-related processes, an additional process seems to contribute to the preferential consolidation of emotional material across sleep (Goldstein and Walker, 2014; Walker and van der Helm, 2009). Various studies have demonstrated that sleep results in the selective enhancement of emotional item memory (Groch et al., 2013; Groch et al., 2015; Hu et al., 2006; Nishida et al., 2008; Payne and Kensinger, 2011; Payne et al., 2008; for a review see Walker and van der Helm, 2009). This enhancement of emotional item memory has been found to be positively correlated with rapid eye movement (REM) sleep duration (Groch et al., 2013; Nishida et al., 2008; Payne et al., 2015) and the proximity of REM sleep onset (Nishida et al., 2008). Furthermore, emotional memory retention has been linked to unique features of REM sleep physiology, specifically to the density of rapid eye movements (Gilson et al., 2015) and theta oscillations (4-7 Hz; Nishida et al., 2008; Prehn-Kristensen et al., 2013). Based on these findings, theta oscillations and particularly their local (right-frontal) topographical distribution have been proposed to reflect reactivations and subsequent reprocessing of affectively relevant events within limbic structures and neocortical networks (Walker and van der Helm, 2009).

It is currently unresolved whether REM-sleep-related reprocessing unfolds in a sequential manner and thus produces additive effects on top of consolidation benefits of prior SWS (for evidence on this view see e.g. Wiesner et al., 2015) or whether emotional item information is primarily consolidated during REM sleep. Recent findings suggest that SWS-rich sleep in the first night half (Groch et al., 2015) and nap sleep (Alger and Payne, 2016) may be associated with a retention benefit for neutral material, which is not evident for emotional material. These selective effects may be accounted for by enhanced learning intention for neutral stimuli. When presented in a task procedure comprising emotional material, neutral stimuli may be perceived as less salient and less memorable (Hourihan et al., 2017) resulting in a stronger effort towards deep-level encoding (Alger and Payne, 2016). These effects may be counteracted when learning intention is enhanced for both emotional and neutral stimuli by providing motivational incentives (Groch et al., 2015). Although requiring further investigation, sequential effects of SWS and REM sleep on emotional memory consolidation may thus be evident in task procedures that actively strengthen intentional processing and hence SWS-related "tagging" of emotional material.

Another outstanding question concerns the types of information consolidated during REM sleep. Specifically, it remains unclear whether REM-sleep-related processes only contribute to the consolidation of emotional item memory or whether their impact extends to the consolidation of emotional associative memory. Previous studies did not find a facilitating effect of sleep on emotional associative and source memory (e.g. Lewiset al., 2011). However, these studies were not suited to reveal differential effects of SWS and REM sleep as they examined memory performance across a full night of sleep without analyzing microstructural features of both sleep stages (esp. REM sleep theta power). In a recent study, we investigated the effects of first night half SWS-rich sleep and second night half REM-sleep-rich sleep on emotional source memory consolidation (Soppet al., 2017). Our results suggest that SWS during the first night half improves retention of neutral, but not emotional, source memory. Moreover, we found a selective retention benefit for emotional source memory across the second night half, which was correlated with a specific oscillatory feature of REM sleep, i.e. right-frontal theta lateralization. As such, behavioral and neurophysiological findings regarding the second night half provide preliminary evidence for the consolidation of emotional

source memory during REM sleep. However, these findings should not be generalized to a broader range of associative item features without further investigations. Importantly, in our previous study, only item location was probed during the memory task. However, theoretical frameworks assume that intrinsic features such as item location may be processed in a stimulus-bound manner (Chiuet al., 2013), thereby gaining access to facilitated perceptual integration during emotional item encoding (Kensinger, 2009; Murray and Kensinger, 2013). Correspondingly, Bennion et al. (2017) found consolidation benefits across REM sleep to be associated with activation changes in the same processing regions which enable facilitated perceptual integration. Consequently, REM-sleep-related consolidation may be restricted to intrinsic features of emotional stimuli. The enhancing effects of REM sleep which emerged in our previous study design could thus potentially rely on the encoding of a strictly intrinsic item feature.

In order to explore this possibility, the current study examined whether similar REM-sleep-dependent effects would emerge for the consolidation of extrinsic features, which are not processed in a stimulus-bound manner. To this end, we employed a paired-associate task in which participants were instructed to encode arbitrary pairs of neutral objects and neutral/emotional background scenes. This change in feature manipulation allowed us to examine the boundary conditions of our previous findings and to further explore the interactions of emotional associative memory encoding and REM-sleep-dependent consolidation. To extend our previous design, we investigated further consolidation-related effects of REM sleep and SWS in a circadian-controlled early morning nap paradigm (see Deliens etal., 2013; Gilson et al., 2015). Participants were asked to discriminate old, recombined and new object-scene pairs prior to (pretest) and following (posttest) a nap opportunity or continued wakefulness (wake control group). In order to link post-sleep memory performance to specific sleep stages, we examined oscillatory EEG features of REM sleep (right-frontal theta lateralization) as well as non-rapid eye movement (NREM) sleep (sleep spindle density). By ascertaining memory performance after a subsequent night of sleep (delayed posttest), we aimed to provide additional insights into the temporal characteristics of sleeprelated memory consolidation. In line with previous studies, we expected to find an enhanced retention of emotional item memory in the nap group (Groch et al., 2013; Nishida et al., 2008; Payne et al., 2015). Moreover, we hypothesized that sleeping during the critical consolidation phase should benefit the retention of both neutral and emotional associative memory. Based on our previous findings (Sopp et al., 2017), we expected to find a neurophysiological dissociation between these retention benefits for emotional and neutral associations: While post-sleep neutral associative memory should be selectively correlated with NREM sleep spindle density, post-sleep emotional associative memory was expected to be selectively correlated with right-frontal theta lateralization during REM sleep.

2. Results

2.1. Sample characteristics

2.1.1. General characteristics

Participants were allocated to a post-encoding nap group and a post-encoding wake group. Nap and wake group participants were comparable in sleep-, mood-, and performance-related measures (see Table 1). However, groups differed in mean age (t_{44} = 2.44, p = .019), which was accounted for by introducing age as a mean-centered covariate in all subsequent between-group analyses. Standard ANOVA results (significant main and interaction effects) are reported in corresponding footnotes.

Table 1	
Group means of state and	l trait characteristics.

Measure	Nap group $(N = 23)$	Wake group $(N = 23)$
State		
KSS Encoding	3.57 (0.84)	$2.96~(0.98)^{*}$
KSS Pretest	3.83 (0.72)	3.57 (1.12)
KSS Posttest	2.52 (0.99)	3.00 (0.85)
KSS Delayed Posttest	2.17 (0.72)	2.04 (0.56)
STADI-S Encoding	33.30 (5.23)	31.00 (5.24)
STADI-S Pretest	35.87 (7.17)	32.65 (6.56)
STADI-S Posttest	31.22 (5.12)	30.09 (4.70)
STADI-S Delayed Posttest	31.61 (7.54)	$27.78(3.57)^{*}$
Trait		
Gender	ੋ:11, ੂ:12	ೆ:10, ⊊:13
Age	22.46 (2.60)	24.31 (2.54)*
IQ (WMT)	10.00 (3.55)	10.91 (2.79)
Verbal Memory (VVM)	8.91 (3.53)	8.96 (3.61)
Sleep Quality (PSQI)	3.26 (1.32)	2.78 (1.35)
Sleepiness (ESS)	5.30 (3.10)	5.83 (3.49)
Chronotype (rMEQ)	13.26 (2.75)	13.43 (2.98)
Trait Anxiety (STADI-T)	19.52 (5.76)	17.78 (5.01)
Trait Depression (STADI-T)	17.87 (5.19)	16.61 (4.61)

Note. KSS = Karolinska Sleepiness Scale, KSS scores range from 1 to 5; STADI = State-Trait Anxiety Depression Inventory, STADI-T anxiety and depression scores range from 10 to 40, STADI-S scores range from 20 to 80; WMT = Wiener Matrizen Test [Viennese matrices test], WMT scores range from 0 to 18; VVM = Visueller und Verbaler Merkfähigkeitstest [Visual and verbal retention test - verbal subtest], VVM scores range from 0 to 24, PSQI = Pittsburgh Sleep Quality Index, PSQI scores range from 0 to 21; ESS = Epworth Sleepiness Scale, ESS scores range from 0 to 24; rMEQ = reduced Morningness-Eveningness questionnaire, rMEQ scores range from 4 to 25. For state sleepiness (KSS) non-parametric test statistics are reported. 'indicates p = .05. Standard deviations are given in parentheses.

State measures of mood (STADI-S) and sleepiness (KSS) were obtained prior to the onset of each phase of the experiment. Groups differed in state sleepiness prior to the encoding phase (U = 177, p = .04) with the nap group reporting higher sleepiness levels (Mdn = 4.00) compared to the wake group (Mdn = 3.00). However, this difference is not in line with the behavioral effects we observed at pre-, post and delayed posttest. Moreover, correlation analyses between state sleepiness at encoding and performance rates at all times of measurements did not yield any significant results (all r > -.23, all p > .110). Current mood states were comparable between groups with the exception of delayed posttest assessment. Nap group participants reported elevated levels of anxious and depressed mood as compared to control subjects (t_{44} = 2.20, p = .033). However, mood state at delayed posttest as measured by the STADI-S was unrelated to item and associative memory performance across the whole experiment (all r < .26, all p > .080).

Table 2

Means of sleep characteristics before and after the main experiment

2.1.2. Pre- and post-experimental sleep characteristics

Sleep was monitored using objective (Fitbit accelerometers) and subjective (sleep diaries) measures during the night before encoding (pre-experimental) and during the night before delayed testing (post-experimental; see Table 2). Objective total sleep time (TST) was estimated to be quite low. However, this may be accounted for by Fitbit's sensitive sleep mode setting, which was used to reduce the rate of false positive epochs (see Meltzer et al., 2015). Between-group analyses of objective and subjective sleep data (Fitbit and sleep diary) did not reveal significant differences at pre-experimental (all t < 1.01, all p > .31) or at post-experimental assessment (all t < 1.60, all p > .12).

Previous findings demonstrate that sleep loss impacts subsequent encoding of emotional material (Kaida et al., 2015). Thus, we examined potential confounding effects of pre-encoding sleep duration on behavioral performance and on correlations between sleep physiology and behavioral performance. Analyses confirmed that all findings concerning pre- and post-sleep memory performance (reported in Sections 2.2.1, 2.2.2, 2.3.2 and 2.3.3) remain unchanged when accounting for objective and subjective pre-experimental sleep duration.

2.1.3. Experimental sleep characteristics

Descriptive statistics of sleep characteristics in the nap group are summarized in Table 3. It is important to note that, as expected (see Section 4.2.), REM sleep duration was higher than in a standard afternoon nap paradigm (e.g. M = 2.76 min in the study of Studte et al., 2017). Nevertheless, REM sleep duration was substantially lower than commonly observed during the second half of nocturnal sleep (e.g. M = 33.44 min in Sopp et al., 2017).

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Sleep parameters	Time in min	% TST
Wake	25.35 (19.67)	
N1	12.35 (9.19)	13.58 (9.10)
N2	53.10 (16.08)	57.17 (13.32)
N3	10.81 (9.48)	12.45 (11.45)
REM	17.22 (13.70)	16.81 (12.74)
TST	93.48 (19.84)	

Note. N1 = NREM Stage 1, N2 = NREM Stage 2, N3 = NREM Stage 3 (corresponding to SWS), REM = REM sleep, TST = total sleep time. Standard deviations are given in parentheses.

Variables	Pre-experimental		Post-experimental		
	Nap	Wake	Nap	Wake	
Fitbit					
TIB (min)	358.09 (13.72)	360.57 (7.65)	469.39 (86.43)	491.91 (57.97)	
TST (min)	264.65 (83.14)	240.39 (80.17)	324.22 (129.74)	314.82 (95.73)	
# of awakenings	6.43 (5.54)	6.04 (5.45)	6.39 (4.80)	8.14 (9.82)	
Sleep diary					
TIB (min)	357.09 (7.76)	357.87 (5.74)	454.68 (81.69)	486.26 (49.45)	
TST (min)	332.55 (56.83)	336.65 (21.56)	450.50 (86.98)	480.00 (45.88)	
SOL (min)	16.76 (12.15)	15.87 (11.74)	13.90 (8.20)	14.00 (16.87)	
WASO (min)	10.44 (14.69)	7.18 (9.45)	0.62 (2.20)	3.60 (8.06)	

Note. Pre-experimental = sleep data for the night prior to encoding; Post-experimental = sleep data for the night prior to delayed posttest; TIB = Time in bed; TST = Total sleep time; SOL = Sleep onset latency; WASO = Wake time after sleep onset. Degrees of freedom vary between analyses as individual participants failed to complete diary questions regarding sleep onset latency and wake time after sleep onset. Standard deviations are given in parentheses.

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Table 4
Adjusted means of memory performance in both groups for item and associative memory.

Performance Measure	Item condition	Nap group (<i>N</i> = 23)			Wake group	Wake group $(N = 23)$		
		Pretest	Posttest	Delayed Posttest	Pretest	Posttest	Delayed Posttest	
PRI	Emotional	.89 (.02)	.84 (.02)	.73 (.03)	.87 (.02)	.82 (.02)	.72 (.03)	
	Neutral	.91 (.02)	.84 (.03)	.75 (.03)	.89 (.02)	.79 (.03)	.75 (.03)	
PR _A	Emotional	.63 (.04)	.51 (.04)	.29 (.03)	.58 (04)	.40 (.04)	.30 (.03)	
	Neutral	.70 (.04)	.58 (.04)	.39 (.03)	.69 (.04)	.46 (.04)	.34 (.03)	

Note. PRI = PR Item memory, PRA = PR Associative Memory. Standard errors of the mean are given in parentheses.



Fig. 1. Adjusted means of associative memory performance (PR_A) for emotional and neutral items in the nap group and wake group at pre-, post- and delayed posttest. *Note.* *indicates significant between-group comparisons. Significant effects between item categories (neutral and emotional) are not illustrated for reasons of comprehensibility. Error bars represent standard error of the mean.

2.1.4. A-priori comparison of memory performance

To examine potential between group performance differences prior to the experimental manipulation, pretest performance rates were subjected to ANCOVAs (see Table 4). Analyses of associative memory performance did not yield a main effect of Group ($F_{1,43} = 0.41$, p = .528) or an interaction between Emotion and Group ($F_{1,43} = 0.79$, p = .379). However, a main effect of Emotion ($F_{1,43} = 23.54$, p < .001) was evident, reflecting significantly higher associative recognition rates for neutral object-scene-pairs as compared to pairs entailing an emotional scene. Analyses of item memory performance did not yield any indication of a-priori differences between groups (main effect of Group: $F_{1,43} = 0.49$, p = .490; Group × Emotion: $F_{1,43} = 0.00$, p = .991). Notably, emotionality of background scenes did not affect item recognition (main effect of Emotion: $F_{1,43} = 2.44$, p = .126) as found with regard to associative memory.

2.2. Behavioral findings

2.2.1. Associative memory

Our main analyses of associative memory performance (preand posttest) yielded significant effects of Time ($F_{1,43} = 131.27$, p < .001), Emotion ($F_{1,43} = 27.88$, p < .001) as well as a significant interaction of Time and Group ($F_{1,43} = 8.16$, p = .007). In accordance with a-priori analysis (see Section 2.1.3), emotionality of background scenes exerted an unexpected detrimental effect on associative memory performance for object-scene pairs. Importantly, this effect was found irrespective of time, with no consolidation benefit emerging for emotional pairs (Time × Emotion: $F_{1,43} =$ 0.66, p = .420).

The main effect of Time reflected a significant decline of performance rates from pre- to posttest. However, this decline was modulated by the factor Group. In line with our hypothesis performance decrements were more pronounced in control subjects ($F_{1,21} = 88.42$, p < .001, d = 2.16) than in subjects of the nap group ($F_{1,21} = 28.08$, p < .001, d = 1.26). This was also mirrored by a significant between-subject difference in performance at posttest ($F_{1,43} = 6.23$, p = .016), which was not evident at pretest ($F_{1,43} = 0.41$, p = .528; see Fig. 1). Analyses did not yield a main effect of Group ($F_{1,43} = 2.69$, p = .108) or any further interaction involving the Group factor (Group × Emotion: $F_{1,43} = 0.13$, p = .724; Group × Time × Emotion: $F_{1,43} = 0.67$, p = .418).¹

2.2.2. Item memory

Analyses of item memory performance revealed a main effect of Time ($F_{1,43} = 28.78$, p < .001; see Fig. 2) reflecting a significant decline in memory performance from pre- to posttest (d = 0.80). Notably, a main effect of Emotion ($F_{1,43} = 0.01$, p = .916) in the direction observed for associative memory performance was not evident. Thus, emotion exhibited differential effects on item and associative recognition, rather than modulating both qualities of memory retention in a similar way.

However, neither emotion nor sleep was found to preserve item memory performance across time as evidenced by a lack of further main or interaction effects (main effect of Group: $F_{1,43} = 1.36$, p = .249; Time × Emotion: $F_{1,43} = 3.70$, p = .061; Time × Group: $F_{1,43} = 0.60$, p = .445; Emotion × Group: $F_{1,43} = 0.43$, p = .517; Time × Emotion × Group: $F_{1,43} = 0.56$, p = .460).² On a descriptive

¹ Significant main and interaction effects without age as covariate: Time: $F_{1,44}$ = 131.80, p < .001; Emotion: $F_{1,44}$ = 28.17, p < .001; Time × Group: $F_{1,44}$ = 7.37, p = .009

² Significant main and interaction effects without age as covariate: Time: $F_{1,44} = 29.30$, p < .001



Fig. 2. Adjusted means of item memory performance for emotional and neutral images at pre-, post- and delayed posttest. *Note.* Performance rates are collapsed across groups. Error bars represent standard error of the mean.

level, emotional item memory performance exhibited a slightly attenuated decline from pre- to posttest (M = 0.05, SD = 0.10) as opposed to neutral item memory performance (M = 0.09, SD = 0.11). However, this difference was not statistically reliable as indicated by the absence of a significant interaction effect.

2.2.3. Post experimental reassessment of memory performance

In order to reexamine potential sleep-related effects on memory performance after a delay without any experimental manipulation, we analyzed performance changes from post- to delayed posttest. Analyses of associative memory performance yielded significant main effects of Time ($F_{1,43}$ = 74.62, p < .001) and Emotion ($F_{1,43}$ = 18.53, p < .001), paralleling the effects observed in the former analysis. Moreover, a significant interaction of Time and Group ($F_{1,43}$ = 6.39, p = .015) emerged, reflecting that performance differences between both groups dissolved from post- to delayed posttest. Accordingly, the significant performance benefit of the nap group at posttest ($F_{1,43}$ = 6.23, p = .016) was not maintained across a subsequent night of sleep ($F_{1,43} = 0.21$, p = .649). Emotional objectscene pairs did not exhibit any delayed retention benefit in terms associative recognition (Time \times Emotion: $F_{1,43}$ = 0.001, of p = .980). Further, no main effect of Group ($F_{1,43} = 2.97$, p = .092) or any further interaction involving the Group factor emerged in these analyses (Emotion × Group: $F_{1,43} = 1.24$, p = .273;Time × Emotion × Group: $F_{1,43} = 0.53$, p = .472).³

Item memory performance, which was not modulated by nap sleep in the former analyses, solely exhibited a significant decline from post- to delayed posttest (main effect of Time: $F_{1,43} = 45.54$, p < .001) with no further main (Group: $F_{1,43} = 0.47$, p = .496; Emotion: $F_{1,43} = 0.02$, p = .895) or interaction effects (Time × Emotion: $F_{1,43} = 2.17$, p = .148; Time × Group: $F_{1,43} = 2.23$, p = .143; Emotion × Group: $F_{1,43} = 0.22$, p = .643; Time × Emotion × Group: $F_{1,43} = 0.49$, p = .487).⁴

2.3. Neurophysiological findings

2.3.1. Correlations between memory performance and sleep stage durations

In summary, behavioral analyses revealed a beneficial effect of nap sleep on associative recognition of both emotional and neutral object-scene-pairs. To explore potential correlations between specific sleep stages and post-sleep memory performance in the nap group, correlations were computed between emotional and neutral item and associative memory and time spent in SWS and REM sleep as well as TST. None of these analyses yielded significant results with respect to post- and delayed posttest performance (all r < .22, all p > .319; see also Supplementary Table A). Thus, we were not able to confirm a selective correlation between posttest emotional item memory performance and REM sleep duration ($r_{23} = -.32$, p = .138), which contradicts prior findings (Groch et al., 2013; Nishida et al., 2008; Payne et al., 2015).

2.3.2. Correlations between memory performance and spindle density (NREM sleep)

2.3.2.1. Pre- and posttest correlations. In a subsequent step, we examined potential correlations between behavioral performance and NREM spindle density in the nap group. Analyses of pretest performance yielded significant correlations between spindle density and both emotional (r_{23} = .60, p = .002) and neutral (r_{23} = .44, p = .034) associative memory. However, analyses of posttest performance only revealed a significant correlation between spindle density and neutral associative memory (r_{23} = .50, p = .014). Spindle density was thus not correlated with posttest emotional associative memory performance (r_{23} = .13, p = .569; see Fig. 3). These correlations were also confirmed to differ on a statistical level $(z_{23} = 1.96, p = .025^5)$. Pretest correlations, on the other hand, did not differ significantly ($z_{23} = 1.14$, $p = .125^6$). To explore the extent to which posttest correlations were modulated by performance at pretest, we conducted a partial correlation analysis between posttest neutral associative memory performance and spindle density with pretest neutral associative memory performance as covariate. This correlation failed to reach significance (r_{20} = .28, p = .210). However, it is important to point out the high proportion of common variance between associative memory at both time points ($r_{23} = .80, p < .001$), which impedes a dissociation of effects by means of partial correlation analyses (for similar results see Studte et al., 2015).

As current frameworks of systems consolidation (Diekelmann and Born, 2010) focus on the role of SWS and assume a differential involvement of fast and slow spindles during this stage (Mölle et al., 2011), we conducted additional correlation analyses between slow (11.0-13.0 Hz) and fast (13.0-15.0 Hz) spindle power (SWS) and posttest memory performance. These analyses yielded a significant correlation between right-frontal (F4) fast spindle power and posttest neutral associative memory (r_{21} = .49, p = .025). In line with correlations between spindle density and posttest memory performance, fast spindle power (F4) was not significantly correlated with posttest emotional associative memory performance $(r_{21} = .16, p = .493)$. Moreover, correlations were found to differ between both valence categories ($z_{21} = 1.66$, p = .048'). Analyses of pretest performance did not reveal significant correlations between fast spindle power (F4) and either emotional (r_{21} = .42, p = .057) or neutral ($r_{21} = .41$, p = .061) associative memory. However, partial correlation analyses between posttest neutral associative memory performance and fast spindle power (F4) with pretest neutral associative memory performance as covariate failed to reach significance (*r*₁₈ = .28, p = .223).

2.3.2.2. Delayed posttest correlations. We analyzed correlations between spindle density (NREM) and delayed posttest performance to examine whether posttest differences in the strength of correlations for emotional and neutral stimuli would be retained

³ Significant main and interaction effects without age as covariate: Time: $F_{1,44}$ = 73.51, p< .001; Emotion: $F_{1,44}$ = 18.66, p < .001; Time × Group: $F_{1,44}$ = 4.86, p = .033

 $^{^4}$ Significant main and interaction effects without age as covariate: Time: $F_{1,44}{=}$ 45.54, $p{<}.001$

⁵ One-sided calculation according to Eid, Gollwitzer, and Schmitt (2010); Correlation between emotional and neutral associative memory at posttest: r_{23} = .58. p= .004

⁶ Correlation between emotional and neutral associative memory at postest r_{23} (5, p) for r_{23} (5, p) for r_{23} (7, 1, p) (0, 1) r_{23} (7, 1)

⁷ Correlation between emotional and neutral associative memory at posttest: $r_{21} = .58$, p = .006



Fig. 3. Correlations between posttest associative memory performance for (A) neutral and (B) emotional object-scene-pairs and spindle density during NREM (mean number of spindles per epoch) in the nap group.



Fig. 4. Correlations between delayed posttest associative memory performance for (A) neutral and (B) emotional object-scene-pairs and spindle density during NREM (mean number of spindles per epoch) in the nap group.

across an additional night of sleep. In line with posttest correlations, spindle density was significantly correlated with neutral associative memory performance at delayed posttest ($r_{23} = .44$, p = .035) whereas the correlation between spindle density and emotional associative memory performance failed to reach significance ($r_{23} = .32$, p = .134; see Fig. 4). However, the strength of these correlations did not differ significantly between both valence categories ($z_{21} = 0.53$, $p = .297^8$). Moreover, partial correlation analyses between delayed posttest neutral associative memory performance and spindle density with pretest neutral associative memory performance as covariate failed to reach significance ($r_{20} = .34$, p = .124).

Analyses of item memory at all times of measurement did not yield a consistent pattern of correlations between memory performance and spindle density. The only significant correlation was found between spindle density and neutral item memory performance at delayed posttest (r_{23} = .47, p = .024). As this remained an isolated finding, it may likely reflect a certain level of shared variance between item and associative memory performance in our combined task procedure.

2.3.3. Correlations between memory performance and theta power (REM sleep)

Based on the findings of Nishida et al. (2008) and our previous results (Sopp et al., 2017), we examined correlations between emotional associative memory performance and right-frontal theta lateralization during REM sleep [F4-F3]. Contrary to our hypothesis, theta lateralization at frontal recording sites was not significantly correlated with posttest emotional associative memory ($r_{17} = -.12$, p = .647). Likewise, neither item nor associative memory of either valence category across all three time points of measurement was significantly correlated with right-frontal theta lateralization (all r < .36, all p > .160). We additionally explored correlations between memory performance and other features of REM sleep physiology (REM sleep latency and REM density), which have been implicated in emotional memory processing (Corsi-Cabrera et al., 2016; Nishida et al., 2008). However, in line with findings for theta laterality, neither of these parameters was

 $^{^8}$ Correlation between emotional and neutral associative memory at delayed posttest: r_{21} = .37, p = .082

significantly correlated with memory performance (see Supplementary Data A).

3. Discussion

The current study examined the effects of an early morning nap on emotional and non-emotional item and associative memory performance. Nap sleep was found to benefit associative memory whereas item memory was similarly retained across wakefulness. Further analyses of specific oscillatory features of NREM, SWS, and REM sleep revealed significant correlations between spindle density (NREM), spindle power (SWS), and neutral associative memory performance at posttest. Emotional associative memory was not related to any micro- or macrostructural parameters of REM sleep physiology.

3.1. Effects of emotion on memory performance

Interestingly, item memory for emotional object-scene pairs did not exhibit a reliable retention benefit across time in both experimental conditions. By contrast, analyses of associative memory performance revealed a significant impairment concerning the successful retrieval of object-scene associations when the respective scene was from the negative and highly arousing stimulus category regardless of time and sleep. We believe that this detrimental effect of emotion may have been related to processes in the initial encoding phase. Specifically, attention during encoding may have been narrowed to the highly arousing scene (Easterbrook, 1959), limiting resources required for successful binding of the objectscene-association. However, as our task design was focused on providing a comprehensive assessment of associative memory performance, it is not possible to infer how memory performance for isolated background scenes was modulated by emotionality. Consequently, accurate recognition of emotional background scenes may have been impeded due to conflicting memory signals elicited by superimposed objects, which may have been impacted by attentional capture of emotional background scenes during encoding. To substantiate the claim that emotional backgrounds elicited an effect of attentional narrowing at encoding and that this resulted in diminished memory for emotional object-scene associations, we conducted a follow-up experiment. We predicted that memory performance should be enhanced for emotional scenes when these are probed independently of superimposed objects but should be impaired for the association of both constituents.

3.1.1. Follow-up experiment

We tested these hypotheses in a follow-up experiment by maintaining the previous encoding procedure but introducing a modified testing procedure. During test trials, participants were asked to discriminate "old" and "new" background scenes. Whenever participants indicated that a scene was "old", a superimposed object was presented. Participants were then instructed to indicate whether the respective scene was previously presented with the displayed objects (yes) or alongside a different object (no). Participants (N = 21) were subjected to this sequential retrieval task prior to and following an interval of wakefulness (2.5 h) during the day. Analyses of independent estimates of item and associative memory yielded the predicted pattern of results: While associative memory was impaired for pairs entailing an emotional scene (Emotion: $F_{1,20} = 15.32$, p = .001), item memory of isolated emotional scenes was significantly enhanced (Emotion: $F_{1,20} = 4.54$, p = .046). The results of our follow-up experiment are thus in line with the interpretation that negative and highly arousing scenes induced attentional narrowing at encoding in the current pairedassociate task (for details of the study design and a full account of the analyses see Supplementary Data B). Although behavioral results support this interpretation, it is important to note that the study did not include any measures of emotional responses to individual images. In order to attribute behavioral effects directly to arousal, future studies should use task formats, which allow the assessment of physiological and subjective emotional responses.

3.2. Effects of sleep on memory performance

Sleep did not yield any beneficial effect on item memory, but produced comparable performance decrements as those observed across wakefulness. This pattern of results does not parallel previous findings of sleep-related enhancements of emotional item memory (e.g. Groch et al., 2013; Nishida et al., 2008; Wiesner et al., 2015). However, it is important to consider that the majority of preceding studies exclusively focused on the assessment of item memory performance. In contrast, the present study used a combined testing procedure of item and associative memory performance, which may account for discrepancies in emotional item memory findings (see also Sopp et al., 2017). In addition, the present study design differs from previous designs, which examined sleep-related effects by using within-subject manipulations (e.g. Hu et al., 2006; Groch et al., 2013; Groch et al., 2015). Our between-subjects design may thus have had limited statistical power to detect differences between item categories across sleep and wakefulness.

However, in line with our predictions, nap sleep resulted in enhanced retention of associative memory for object-scene associations. This pattern of results is consistent with the notion that sleep-dependent consolidation is particularly involved in the maintenance of hippocampus-dependent associative memory (Studte et al., 2015; van der Helm et al., 2011). Supportive evidence that our task required hippocampal binding processes during encoding comes from an fMRI study by Luck et al. (2014). Employing a similar task design, the authors found that successfully retained - as opposed to subsequently forgotten - object-scene pairs elicited enhanced hippocampal activation during encoding. These results confirm the relevance of hippocampal processing during successful encoding of relations between objects and scenes in this particular type of paired-associate task.

3.2.1. Neurophysiological correlates of behavioral performance

3.2.1.1. Correlations between NREM sleep features and memory performance. The sleep-related enhancement of associative memory performance was evident across both negative and neutral scenes. In order to investigate the link between enhancements in neutral associative memory performance and NREM-sleepdependent consolidation processes, we examined correlations between spindle density and pre-, post- and delayed posttest performance. Results revealed significant and positive correlations between pretest associative memory performance of both valence categories and subsequent spindle density. This correlation of spindle density and memory performance prior to the onset of any putative effects of sleep-related consolidation may reflect a distinct "trait-like" characteristic of spindle density (for similar findings see Gais et al., 2002; Studte et al., 2015; Studte et al., 2017). Current accounts propose that spindle density can be regarded as a physiological index of intelligence (Fogel and Smith, 2011). Spindle correlations with pretest performance may thus reflect the close link between general cognitive abilities and memory performance. In order to dissociate trait- and consolidation-related variance, individual spindle density has to be determined in a baseline night before the experimental learning task is administered (see e.g. Fogel et al., 2007; Schabus et al., 2007, 2008). Alternatively, causal effects of spindle activity can be established by examining learning-related increases in spindle density across learning and non-learning conditions (Gais et al., 2002). Accordingly, in the current design, conclusions regarding the contribution of spindle density to memory consolidation must remain tentative.

Notably, analyses at posttest revealed a differential pattern of correlations: Posttest associative memory performance was correlated with spindle density for neutral but not for emotional objectscene pairs. On the basis of a purely trait-based account, one would predict stable correlations between spindle density and associative memory performance across time. Our results are thus not easily explained by trait-related differences in spindle density. Moreover, differential correlations were also confirmed in SWS-based analyses. Taken as a whole, these findings may suggest that NREM-sleepdependent consolidation processes contributed to the retention of neutral object-scene associations, whereas this contribution was weaker for emotional associations. Although this interpretation is limited by the lack of significant results in partial correlation analyses, it is important to consider consistencies with previous findings. As such, early night SWS-rich sleep has been found to benefit neutral, but not emotional source recognition (Groch et al., 2015; Sopp et al., 2017; but see Lewis et al., 2011 for different findings).

One potential explanation which may account for these selective benefits is that arousal attenuates SWS-related tagging mechanisms. Tagging mechanisms are assumed to enable systems consolidation during SWS by initiating reactivation and subsequent redistribution of memory representations between different subsystems (Diekelmann and Born, 2010). A growing body of research indicates that tagging relies on the strength of learning intention during initial encoding (Rasch and Born, 2013). Thus, it may be speculated that the salience of emotional material dampens learning intention (Fairfield et al., 2015; Hourihan et al., 2017) to the extent that emotional associations are less likely to be reactivated during subsequent SWS. This line of reasoning may also account for the variable contributions of SWS to emotional memory consolidation in the literature (see e.g. Wiesner et al., 2015). These contributions may be contingent on the degree to which individual task instructions enforce learning intention for emotional material (e.g. by providing monetary incentives; see Groch et al., 2015 for complemental evidence).

Another potential explanation for the present pattern of results is that arousal impaired sleep-related consolidation by disrupting encoding processes. Hence, differential spindle correlations may have emerged due to weaker encoding of emotional material as evident in pretest performance rates. Indeed, certain findings suggest that weak encoding may reduce subsequent benefits of sleeprelated consolidation (Creery et al., 2015; Schmidt et al., 2006; but see Drosopoulos et al., 2007). These effects may emerge because successful reactivation during sleep requires deep level integration during associative memory encoding (Schmidt et al., 2006). Conversely, weak encoding may result in a failure of reactivation or in the strengthening of erroneous memory representations (Creery et al., 2015). Hence, spindle density, a marker of reactivation, may be uncorrelated with post-sleep emotional associative memory as a consequence of weak encoding due to attentional narrowing. Importantly, this interpretation accounts for overall impaired emotional associative memory, which was not similarly evident in previous studies (Groch et al., 2015; Sopp et al., 2017) and cannot be attributed to potential differences in learning intention (see similar performance rates in Hourihan et al., 2017).

Overall, both explanations assume that differential spindle correlations do not result from the processing of arousing stimuli per se, but from indirect effects of arousal on mnemonic processing. However, future research is required to address whether these indirect effects are related to learning intention or to weaker encoding (e.g. by manipulating learning intention as well as strength of encoding for emotional associations). Moreover, as partial correlations controlling for pretest performance failed to reach significance, future studies should seek to examine differential correlations between spindle density and pre- and post-sleep memory performance in larger samples. These may yield sufficient statistical power to detect moderately large partial correlations resulting from strongly correlated pre- and post-measures.

3.2.1.2. Correlations between REM sleep features and memory performance. Although memory for both emotional and neutral associations was found to benefit from sleep, posttest emotional associative memory performance was neither correlated with NREM spindle density nor with SWS spindle power. This absence of correlations could be seen as a preliminary, but weak indication that an additional process may have contributed to the consolidation of emotional associations in the current experiment. However, this indication was not substantiated by sleep physiological data, as posttest emotional memory performance was not correlated to right-frontal theta lateralization. Moreover, correlation analyses between other REM sleep parameters (REM sleep duration, latency, and REM density) and emotional memory performance similarly did not reveal any significant correlations (see Supplementary Data A). This discrepancy with regard to previous findings may have emerged due to methodological limitations of the current design. Specifically, the distribution of sleep stages in the morning nap condition (see Section 2.1.2) resulted in restricted interindividual variance in REM sleep duration, which may account for the absence of a linear relationship between REM sleep macrostructure and emotional item memory performance.

With regard to microstructural analyses, it is important to note that overall REM sleep duration was considerably low in the current experiment (M = 17.33, SD = 13.70). This overall low duration may have restricted us in reliably deriving measures of microstructural sleep architecture (e.g. theta laterality). These restrictions are an inherent issue in nap studies as the short sleep opportunity prevents individual subjects from entering specific stages (esp. REM sleep) or from expressing sufficient numbers of epochs for subsequent analyses (Borbély and Achermann, 1992; Dijk et al., 1997). In the current study, 17 participants entered microstructural analyses of REM sleep physiology, whereas all 23 participants were eligible for spindle density analyses (see Section 4.5.2). Enhanced error variance (e.g. due to few REM epochs of sufficient quality) in the restricted subsample (N = 17) may thus have distorted correlations between emotional memory performance and right-frontal theta lateralization.

By contrast, the absence of correlations between micro- and macrostructural features of REM sleep physiology and posttest emotional memory performance may suggest that REM-sleeprelated consolidation processes are less likely to be initiated for extrinsic features of emotional stimuli. Recurring to our initial study objective, it may be speculated that REM-sleep-related enhancements are, in fact, restricted to the reprocessing of intrinsic source features (such as item location), which have been found to benefit from arousal (Chiu et al., 2013). The arousal-induced impairment of associative memory performance at pretest (see Section 3.1) supports this interpretation as no such effect emerged in our previous experiment (Sopp et al., 2017). As with regard to spindle density, it is thus possible that the arousal-induced disengagement of encoding processes resulted in a subsequent disengagement of REM-sleep-related consolidation processes. Future studies should test this hypothesis by utilizing associative memory tasks, which manipulate extrinsic and intrinsic feature encoding across different trials in the same task procedure. If confirmed, this pattern of results would be in line with the notion that sleep selectively unbinds emotional salient features from complex episodes in order to preserve their most adaptive elements (see e.g. Payne and Kensinger, 2010).

3.3. Effects of sleep on delayed memory performance

We examined whether potential differences resulting from sleep-related consolidation are sustained across time by assessing memory performance after an additional night of sleep. Performance rates at delayed posttest did not differ significantly between the nap and wake group, which may suggest that the effects of sleep on memory performance are short-lived and do not persist against uncontrolled sources of variance outside of laboratory conditions. Alternatively, this lack of persistence may be related to the fact that the current study used a between-subject-design, which limits statistical power. To eliminate this possibility, future designs should employ within-subject designs as these may reveal subtle differences in delayed performance after nap sleep as compared to wakefulness.

In contrast to the null effect between groups at delayed posttest, we found that the correlation pattern between spindle density and associative memory performance was maintained across time. Although differences in the strength of correlations for neutral and emotional associative memory did not reach significance, these findings may suggest that a delayed consolidation took place between post- and delayed posttest sessions in the wake group. Hence, wake group participants may have "caught up" on sleeprelated performance benefits, whereas performance remained to be correlated with the initial neurophysiological signature of nap sleep in nap group participants. This interpretation is in line with previous findings of Schönauer et al. (2015). The authors report a similar pattern of results suggesting a delayed consolidation effect across a three-day retention interval after initial post-learning sleep deprivation. These effects of delayed consolidation may extend previous accounts, which suggest that sleep-dependent consolidation has to occur within a period of 10 h after encoding to prevent memory decay (Gais et al., 2006; Talamini et al., 2008). However, before the current findings are not replicated under controlled laboratory conditions (i.e. including PSG monitoring during delayed sleep), no strong conclusion can be drawn.

3.4. Conclusions

In summary, the current findings demonstrate a beneficial effect of early morning sleep on associative memory. Correlation analyses between memory performance and microstructural sleep features suggest that neutral associative memory exhibits a temporally persistent relationship with NREM-sleep-related oscillatory features. This finding is consistent with increasing evidence that SWS is selectively related to the consolidation of neutral associations although the possibility that correlations underlie trait-related variance in spindle density cannot be fully excluded from the current data. Contrary to our hypotheses, emotional associative memory performance was not linked to any micro- or macrostructural REM sleep parameter. Future research is required to disentangle whether the lack of correlation between emotional associative memory and REM sleep physiology is related to methodological constraints of the current study design or whether it is related to selective benefits of REM-sleep-related processing for intrinsic item features.

4. Experimental procedure

4.1. Subjects

Fifty-three subjects took part in the present study. Study eligibility was confirmed using an online screening survey and a telephone interview. Participation was restricted to individuals fulfilling the following criteria: sufficient sleep quality (PSQI \leq 5; Buysse et al., 1991), no extreme circadian preferences (neither strong eveningness nor strong morningness preference; Randler, 2013), habitual sleep duration ≥ 6 h, absence of regular shift work, and pronounced right-handedness (as determined by Oldfield, 1971). Potentially confounding effects of menstrual cycle were minimized by selecting only females using hormonal contraception. Participants were further required to be native German speakers, aged between 18 and 30 years with normal or corrected-to-normal vision, and to be in good general health (BMI in the normal range, no acute or chronic disorders including mental disorders⁹, previous drug use or long-term medication). Potential participants were excluded from further participation if they scored ≥ 10 on the Patient Health Questionnaire (PHQ-9; Kroenke et al., 2001).

The final sample for analyses comprised 23 participants (11 male; M_{age} = 22.46, SD = 2.60) in the nap condition and 23 participants (10 male; M_{age} = 24.31, SD = 2.54) in the wake condition. Three participants were excluded as they did not meet criteria for required sleep/wake properties. In one subject of the wake group, N2 sleep was detected during the consolidation phase and two participants of the nap group did not show a minimum duration of 30 min NREM sleep. Additionally, three participants were excluded due to insufficient memory performance indicating a lack of compliance with task procedures. Two subjects were excluded due to poor associative recognition performance at pretest (1.5 \times interquartile range below the lower quartile of the overall group) and one further participant was excluded as individual performance in emotional associative memory failed to exceed chance level at posttest. One further participant failed to complete experimental procedures due to premature termination of study participation and was consequently discarded from analyses.

The study was conducted according to the general principles expressed in the Declaration of Helsinki. All participants gave written informed consent and were paid 75 \in for study participation.

4.2. Study design

The present study used an early morning nap manipulation in order to facilitate REM sleep onset and establish a predominance of REM sleep duration (see Fig. 5; Carr and Nielsen, 2015; Deliens et al., 2013; Gilson et al., 2015; Groeger et al., 2011). Three days prior to study participation, subjects were asked to complete baseline measures of trait anxiety and depression (Trait Anxiety and Depression Inventory, STADI; Laux et al., 2013) as well as tests of fluid intelligence (Formann et al., 2011) and verbal memory (Schelling and Schächtele, 2001). Questionnaires and tests were completed in an online survey and were used to compare baseline characteristics of study groups. During the pre-experimental night, participants were asked to restrict their sleep duration to six hours by going to bed at midnight and rising at 6:00 a.m. the latest (see Fig. 5). Adherence to procedures was monitored by accelerometers (Fitbit Flex, Fitbit, Inc.), sleep diary and confirmation of awakening via email. Additionally, participants were asked to refrain from alcohol, caffeine and nicotine intake as well as physical exercise starting 24 h prior to the experiment.

Participants arrived at the laboratory at 8:00 a.m. and were seated in a soundproofed testing booth facing a 27" LCD monitor (60 Hz refresh rate) at a viewing distance of about 65 cm. Thereafter, they conducted the encoding phase of the experiment which was followed by the pretest procedure. Subsequently, participants were prepared for polysomnographic measurements during the succeeding nap (or monitoring of wakefulness during the corresponding interval in the control condition). Group allocation was

⁹ Participants were not subjected to any standardized screening procedure for mental disorders. However, they were asked about mental disorders during the screening interview. If they indicated that they had ever been diagnosed with or sought help for a mental disorder, they were excluded from further participation.



Fig. 5. Overview of the study design. *Note.* In the main experimental phase participants were allocated to the nap or wake group. Dashed time periods designate preparation of polysomnographic measurements (prior to experimental sleep/wake phase) and sleep inertia recovery (following the experimental sleep/wake phase).

determined in a pseudorandom fashion to establish balanced gender ratios in both groups (see Genzel et al., 2012 for accounts of differential sleep-related effects on memory consolidation between genders). Participants were assigned to individual groups before their arrival at the laboratory (during lab preparation at approximately 7:30 a.m.). However, they were informed about their assignment after preparation of polysomnographic measurements (before entering the room, in which they were asked to sleep or, alternatively, remain awake). At approximately 10:30 a.m. subjects of the nap condition obtained a 120-min sleeping opportunity, whereas control participants were instructed to watch a nonarousing, low interfering and non-narrated documentary movie of the daily life in a monastery ("Into Great Silence", Philip Groening) while remaining awake. At the end of the 120-min interval, participants of both groups were seated in the laboratory for 30 min during which they watched excerpts of calming landscapes (taken from "Relaxing: The most beautiful landscapes on earth") and were served a standardized snack and drink. This phase was introduced to prevent potential detrimental effects of sleep inertia on immediate memory performance. Subsequently, participants underwent posttest procedures at approximately 01:00 p.m. which were identical to the initial pretest, but comprised a different set of stimuli. Following completion of the posttest, participants were sent home and instructed to return on the following day at 11:00 a.m. Sleep timing and duration between the two testing days were unrestricted and participants were asked to continue completing the sleep diary and wear their individual accelerometer. On day 2, participants completed the delayed posttest that was identical to pre- and posttest procedures but entailed a different set of stimuli. Measures of state sleepiness (Karolinska Sleepiness Scale, KSS¹⁰; Kaida et al., 2006) and current mood (State Anxiety and Depression Inventory, STADI-S; Laux et al., 2013) were ascertained at the onset of each phase of the experiment (encoding and test phases).

4.3. Memory task

The present task design was similar to the designs used by Ventura-Bort et al. (2016) and Lucket al. (2014). Different object-

scene-pairs were presented during encoding with the instruction to memorize these for a subsequent test phase (see Fig. 6).

4.3.1. Stimulus material

The stimulus material for the current experiment was selected from the International Affective Picture System (Lang et al., 2005) and the Nencki Affective Picture System (Marchewka et al., 2014). Pictures were preselected in order to contrast memory performance for negative, highly arousing scenes (valence: M = 2.56, SD = 0.70; arousal: M = 6.35, SD = 0.71) with memory performance for neutral scenes (valence: M = 5.55, SD = 0.58; arousal: M = 4.14, *SD* = 0.79). All stimuli were rated in a separate sample of participants (N = 10) to preclude substantial deviations from the original norms in the current population. Furthermore, scenes were matched with regard to luminance, animacy, the occurrence of faces and indoor/outdoor scenes both between lists and between valence categories (all p > .20). A total of 243 pictures were selected in each category (neutral and emotional). Pictures were divided into nine parallel sets serving as old, recombined and new scenes at each time of measurement. All subsets of each valence category (neutral and emotional) did not differ significantly in valence or arousal (all p > .57). The assignment of subsets was counterbalanced across participants and the order of stimulus presentation was pseudorandomized individually for each participant with no more than two scenes of the same valence category occurring consecutively.

The objects which were presented in conjunction with emotional and neutral scenes were chosen from the Bank of Standardized Stimuli (BOSS; Brodeur et al., 2014) and from the Alternative Snodgrass and Vanderwart Stimulus Set (Moreno-Martínez and Montoro, 2012). Objects were selected to encompass a variety of different, instantaneously identifiable and inanimate objects from various semantic categories (e.g. tools, furniture, and clothing). Allocation to sublists was performed randomly with subsequent adjustments to prevent an imbalance of specific semantic categories of objects in single lists. In addition, mean stimulus ratings of name agreement, familiarity, visual complexity and manipulability were matched across all 18 lists and likewise between neutral and negative lists (p > .20). Object lists were assigned to sublists of emotional and neutral scenes at random but assignment within lists was manually corrected to ensure no semantic relation between scenes and their respective object. Lastly, the location of the object (upper right, lower right, upper left or lower left) was

 $^{^{10}}$ The original KSS labels were rated on a 5-point-scale (1 = very alert, 2 = alert, 3 = neither alert nor sleepy, 4 = sleepy – but no difficulty remaining awake, 5 = very sleepy – fighting sleep).



Fig. 6. Task design of (A) encoding and (B) test procedures. Note. The test procedure was identical at pre-, post and delayed posttest.

determined pseudorandomly to prevent objects from covering highly relevant aspects of the scene as they were presented in a superimposed manner. Location of object presentation was balanced within each list and across all 18 lists. Each constituent of individual stimulus pairs (scene and object) was re-used to serve in recombined pairs during testing. The individual position of the object was retained across the experiment by creating recombined pairs only between object-scene pairs of the same location and again ensuring no semantic relatedness by the judgment of two independent raters. This process of stimulus generation resulted in two parallel versions (serving as old or recombined pairs respectively) of 18 lists of 27 object-scene-pairs each. Objects and scenes were rescaled to 212×212 pixels and 950×713 pixels respectively. Throughout the experiment, all scenes were presented at a horizontal visual angle of 15.3° and a vertical visual angle of 16.6°. During each phase of the experiment, participants were familiarized with the task procedures by completing four test trials.

4.3.2. Encoding phase

Prior to the encoding phase of the experiment, participants were instructed that they were going to see different scenes in conjunction with simple everyday objects, which they were to remember for a subsequent memory test (see Fig. 6A). It was additionally emphasized that the successful accomplishment of the task would depend on retrieving the explicit association between the scene and its respective object. Each trial began with the presentation of a fixation cross (500 ms) which was succeeded by the presentation of the object in its respective location (1500 ms). Thereafter, the object-scene pair was presented conjointly (3000 ms) together with the instruction to imagine that the object is part of the scene. Following stimulus presentation, participants were asked to rate the plausibility of the object-scene pair (5000 ms) on a scale ranging from 1 (implausible) to 4 (plausible). Trials were separated by an inter-trial interval of 2000 ms and were presented in four blocks with three self-paced pauses interspersed.

4.3.3. Test phases

Following encoding, participants immediately completed the pretest procedure to ascertain baseline memory performance

independent of potential contributions of consolidation processes occurring across sleep or wakefulness (see Fig. 6B). Participants were instructed to differentiate entirely new object-scene pairs from old and recombined pairs. While old pairs were presented in identical composition, recombined pairs comprised an object and a scene that had been presented in conjunction with a different scene or object during initial encoding. This testing procedure allows deriving an index of associative memory, which excludes familiarity-based recognition and thus strongly reflects recollective processes (Yonelinas, 2002). Prior to each test trial, a fixation cross (500 ms) was presented that was succeeded by the presentation of the object-scene pair (3000 ms). Participants were instructed to respond as fast and accurately as possible with the onset of the stimulus by indicating its status relative to the encoding phase (old, new or recombined). At stimulus offset an additional response window was introduced allowing participants to respond for an additional duration of 3000 ms. Subsequently, participants were asked to rate the confidence of their response (5000 ms) on a 4-point-scale (uncertain, rather uncertain, rather certain, certain). The inter-trial interval was set to 2000 ms and stimuli were presented in three blocks.

Post- and delayed posttest procedures were identical to the sequence outlined above but entailed different subsets of stimuli. Participants were explicitly instructed that item status was to be determined relative to the encoding phase and that "new" object-scene-pairs of previous test phases would not reappear in subsequent tests.

4.4. EEG recordings and analyses

In both experimental conditions standard polysomnography recordings (AASM, 2007) were performed including EEG (F3 and F4 according to the international 10–20 system), EMG (submental) and horizontal EOG (lower right and higher left canthi). Signals were digitized at a sampling rate of 256 Hz (EEG and EOG) or 512 Hz (EMG) and amplified by a wireless SOMNOtouch amplifier system (SOMNOmedics GmbH, Randersacker, Germany) which was attached with a centered chest strap. Data were filtered online with a first-order high-pass filter at 0.3 Hz, a second-order Butterworth low-pass filter at 75 Hz and a Notch-filter at 50 Hz. All

electrodes were recorded referenced to Cz and were re-referenced offline to the average of both mastoids. Data of Cz was reinstated during re-referencing. Subsequent sleep stage scoring, spindle analysis, and spectral analyses were based on F3, F4, and Cz. A 0.3–35 Hz bandpass filter was applied offline for sleep stage scoring.

Visual sleep stage scoring was performed independently by two trained raters in accordance with the criteria provided by the AASM (2007) and using the Matlab-based toolbox FASST (fMRI Artefact rejection and Sleep Scoring Toolbox; Leclercq et al., 2011). Epochs (20 s) were scored visually as NREM stages N1-3, stage R and stage W. This epoch length was chosen to allow for overlapping windows of 4 s in the computation of spectral power density. Both the absolute amount of minutes spent in each sleep stage as well as the relative amount with reference to total sleep time (% TST) was determined for descriptive statistics and/or correlation analyses.

For exploratory correlation analyses, we additionally determined REM sleep latency with reference to sleep onset (Nishida et al., 2008) and REM density (Corsi-Cabrera et al., 2016). REMs were detected for each 2-s epoch of REM sleep. First epochs were identified for which activity in either EOG channel exceeded a minimum amplitude threshold of 40 μ V. Thereafter, identified epochs were reviewed visually for well-defined REM-related EOG activity in both EOG channels (for similar approaches see Ficca et al., 2004; Fogel et al., 2007). Detection was performed by a trained research assistant, who was unaware of the research hypotheses and individual performance rates.

4.4.1. Spindle detection and spectral analysis

Spindle density during NREM sleep (N2 and N3) was determined by means of the spindle detection algorithm implemented in the FASST-toolbox based on the method described by Mölle et al. (2002). In brief, the data of all three channels (F3, F4, and Cz) was bandpass filtered (8-20 Hz). Thereafter, the root mean square signal was computed. This signal was then transformed into a binary signal using individually computed spindle thresholds. Spindle thresholds were computed as the 95th percentile of the extracted signal of individual channels scored as stage N2. Using the ceiled average of three binary signals, bursts of activity in the frequency range of interest with a minimum duration of 400 ms were detected and considered as spindles (for a previous study using this algorithm see Ong et al., 2016). These potential spindle events were then reviewed visually and excluded when necessary by a trained research assistant who was unaware of the research hypotheses and individual performance rates.

Spectral analysis was performed using the Matlab-based toolbox EEGLAB (<u>http://www.sccn.ucsd.edu/eeglab/</u>). Spectral power density was computed for each epoch of REM sleep and SWS as previously described in Sopp et al. (2017). For REM sleep epochs, power estimates were averaged in the theta (4.0–7.0 Hz) frequency range (Nishida et al., 2008). Frontal theta lateralization was computed by subtracting theta activity at electrode F3 from that at F4 [F4- F3]. For SWS epochs, power estimates were averaged in the fast (13.0–15.0 Hz) and slow (11.0–13.0 Hz) spindle frequency ranges (Schabus et al., 2007).

4.5. Statistical analyses

4.5.1. Memory task

Performance rates for old, recombined and new object-scene pairs were used to derive two separate measures of item and associative memory performance. Performance scores for item memory $[PR_I = p(Old + Rec|Old) - p(Old + Rec|New)]$ were based on the rate

of pooled "old" and "recombined" responses to old pairs adjusted by the rate of pooled "old" and "recombined" responses to new pairs (Snodgrass and Corwin, 1988). Performance scores for associative memory [PR_A = p(Old|Old) - p(Old|Rec)] were based on the rate of "old" responses to old pairs accounting for the rate of "old" responses to recombined pairs (see Luck et al., 2014 for a similar approach).

Associative and item memory performance scores were subjected to separate ANCOVAs including the within-subject factors Time (pre-/posttest) and Emotion (negative/neutral background scene) as well as the between-subject factor Group (nap/wake group). In order to follow-up on potential sleep-related effects after a subsequent night of sleep, separate ANCOVAs were performed including the within-subjects factors Time (post-/delayed posttest) and Emotion (negative/neutral) as well as the betweensubject factor Group (nap/wake group). Reaction time data were analyzed accordingly but including the additional within-subject factor Item type (Old|Old/Rec|Rec/New|New). Results of reaction time analyses can be found in the supplementary materials (see Supplementary Data C).

4.5.2. Sleep physiology and oscillatory EEG features

To link behavioral effects with specific microstructural aspects of sleep physiology, Pearson correlation coefficients (r) were computed between memory performance (at pre-, post- and delayed posttest) and measures of oscillatory features derived from the analyses described above. Furthermore, correlation analyses were performed with respect to absolute time spent in REM sleep, SWS and TST.

As individual participants failed to reach REM sleep (N = 5) corresponding analyses of REM sleep features were based on remaining subsets of participants. One additional subject was excluded from theta analyses due to a low number of REM epochs (after artifact rejection) which resulted in theta power strongly deviating from the groups' distribution $(3 \times interguartile range below the$ lower quartile of the overall group). This resulted in a subsample of *N* = 17 for REM-sleep-related oscillatory analyses. For REM density analyses, one subject was excluded due to poor signal quality of EOG recordings. Thus, N = 17 participants entered analyses of REM density. All subjects (N = 23) were eligible for analyses of spindle density, whereas analyses of SWS spindle power were restricted to participants entering SWS (N = 21). Significant main effects and interactions were followed by a-priori specified t-tests. For all analyses, the significance level was set to α = .05. For correlation analyses of main outcome measures (theta laterality and spindle density), the Benjamini and Hochberg (1995) procedure for controlling false discovery rate (FDR) was applied with an FDR of 10%.

5. Declaration of interests

None

6. Funding

This work was supported by the German Research Foundation [grant IRTG 1457].

Acknowledgements

We gratefully acknowledge Edith Friesen, Barbara Kiefer, Nina Knieriemen, Lea Kornhas, Pia Muhl, Nicole Pieprzyca, Teresa Schmitz and Omer Schonfeld for assisting with data collection/analyses.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.brainres.2018.06. 020.

References

- AASM, 2007. The AASM Manual for the Scoring of Sleep and Associated Events: Rules, Terminology and Technical Specifications. American Academy of Sleep Medicine, Darien (Illinois)
- Alger, S.E., Payne, J.D., 2016. The differential effects of emotional salience on direct associative and relational memory during a nap. Cogn. Affect. Behav. Neurosci. 16 (6), 1150–1163.
- Baran, B., Daniels, D., Spencer, R.M., 2013. Sleep-dependent consolidation of valuebased learning. PLoS One 8 (10), e75326.
- Benjamini, Y., Hochberg, Y., 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. J. R. Stat. Soc. B 57 (1), 289–300. Bennion, K.A., Payne, J.D., Kensinger, E.A., 2017. Residual effects of emotion are
- reflected in enhanced visual activity after sleep. Cogn. Affect. Behav. Neurosci. 17 (2), 290–304.
- Borbély, A.A., Achermann, P., 1992. Concepts and models of sleep regulation: an overview. J. Sleep Res. 1 (2), 63-79.
- Born, J., Wilhelm, I., 2012. System consolidation of memory during sleep. Psychol. Res. 76 (2), 192–203. Brodeur, M.B., Guérard, K., Bouras, M., 2014. Bank of standardized stimuli (BOSS)
- phase II: 930 new normative photos. PLoS One 9 (9), e106953.
- Buysse, D.J., Reynolds III, C.F., Monk, T.H., Hoch, C.C., Yeager, A.L., Kupfer, D.J., 1991. Quantification of subjective sleep quality in healthy elderly men and women
- using the Pittsburgh Sleep Quality Index (PSQI). Sleep 14 (4), 331–338. Carr, M., Nielsen, T., 2015. Morning REM sleep naps facilitate broad access to
- emotional semantic networks. Sleep 38 (3), 433–443. Chiu, Y.-C., Dolcos, F., Gonsalves, B.D., Cohen, N.J., 2013. On opposing effects of emotion on contextual or relational memory. Front. Psychol. 4, 103.
- Corsi-Cabrera, M., Velasco, F., Río-Portilla, Y., Armony, J.L., Trejo-Martínez, D., Guevara, M.A., Velasco, A.L., 2016. Human amygdala activation during rapid eye movements of rapid eye movement sleep: an intracranial study. J. Sleep Res. 25 (5), 576-582.
- Creery, J.D., Oudiette, D., Antony, J.W., Paller, K.A., 2015. Targeted memory reactivation during sleep depends on prior learning. Sleep 38 (5), 755-763.
- Deliens, G., Leproult, R., Neu, D., Peigneux, P., 2013. Rapid eye movement and nonrapid eye movement sleep contributions in memory consolidation and resistance to retroactive interference for verbal material. Sleep 36 (12), 1875-1883.
- Diekelmann, S., Born, J., 2010. The memory function of sleep. Nat. Rev. Neurosci. 11 (2), 114–126.
- Dijk, D.-J., Shanahan, T.L., Duffy, J.F., Ronda, J.M., Czeisler, C.A., 1997. Variation of electroencephalographic activity during non-rapid eye movement and rapid eye movement sleep with phase of circadian melatonin rhythm in humans. J. Physiol. 505 (3), 851-858.
- Drosopoulos, S., Schulze, C., Fischer, S., Born, J., 2007. Sleep's function in the spontaneous recovery and consolidation of memories. J. Exp. Psychol. Gen. 136 (2), 169–183.
- Easterbrook, J.A., 1959. The effect of emotion on cue utilization and the organization of behavior. Psychol. Rev. 66 (3), 183-201.
- Eid, M., Gollwitzer, M., Schmitt, M., 2010. Statistik und Forschungsmethoden. Beltz, Weinheim (Germany). Fairfield, B., Mammarella, N., Palumbo, R., Di Domenico, A., 2015. Emotional meta-
- memories: a review. Brain Sci. 5 (4), 509–520.
- Ficca, G., Scavelli, S., Fagioli, I., Gori, S., Murri, L., Salzarulo, P., 2004. Rapid eye movement activity before spontaneous awakening in elderly subjects. J. Sleep Res. 13 (1), 49-53.
- Fogel, S.M., Smith, C.T., 2011. The function of the sleep spindle: a physiological index of intelligence and a mechanism for sleep-dependent memory consolidation. Neurosci. Biobehav. Rev. 35 (5), 1154–1165.
- Fogel, S.M., Smith, C.T., Cote, K.A., 2007. Dissociable learning-dependent changes in REM and non-REM sleep in declarative and procedural memory systems. Behav. Brain Res. 180 (1), 48-61.
- Formann, A.K., Piswanger, K., Waldherr, K., 2011. Wiener Matrizen-Test 2: Ein Rasch-skalierter sprachfreier Kurztest zur Erfassung der Intelligenz. Beltz, Weinheim (Germany).
- Gais, S., Mölle, M., Helms, K., Born, J., 2002. Learning-dependent increases in sleep spindle density. J. Neurosci. 22 (15), 6830–6834.
- Gais, S., Lucas, B., Born, J., 2006. Sleep after learning aids memory recall. Learn. Mem. 13 (3), 259-262.
- Genzel, L., Kiefer, T., Renner, L., Wehrle, R., Kluge, M., Grözinger, M., Dresler, M., 2012. Sex and modulatory menstrual cycle effects on sleep related memory consolidation. Psychoneuroendocrinology 37 (7), 987-998.
- Gilson, M., Deliens, G., Leproult, R., Bodart, A., Nonclercq, A., Ercek, R., Peigneux, P., 2015. REM-enriched naps are associated with memory consolidation for sad stories and enhance mood-related reactivity. Brain Sci. 6 (1), 1–18.
- Goldstein, A.N., Walker, M.P., 2014. The role of sleep in emotional brain function. Annu. Rev. Clin. Psychol. 10, 679-708.

- Groch, S., Wilhelm, I., Diekelmann, S., Born, J., 2013. The role of REM sleep in the processing of emotional memories: evidence from behavior and event-related potentials. Neurobiol. Learn. Mem. 99, 1-9.
- Groch, S., Zinke, K., Wilhelm, I., Born, J., 2015. Dissociating the contributions of slow-wave sleep and rapid eye movement sleep to emotional item and source memory. Neurobiol. Learn. Mem. 122, 122-130.
- Groeger, J.A., Lo, J.C., Burns, C.G., Dijk, D.-J., 2011. Effects of sleep inertia after daytime naps vary with executive load and time of day. Behav. Neurosci. 125 (2), 252-260.
- Heib, D.P.J., Hoedlmoser, K., Anderer, P., Gruber, G., Zeitlhofer, J., Schabus, M., 2015. Oscillatory theta activity during memory formation and its impact on overnight consolidation: a missing link? J. Cognit. Neurosci. 27 (8), 1648-1658.
- Hourihan, K.L., Fraundorf, S.H., Benjamin, A.S., 2017. The influences of valence and
- arousal on judgments of learning and on recall. Mem. Cognit. 45 (1), 121–136.
 Hu, P., Stylos-Allan, M., Walker, M.P., 2006. Sleep facilitates consolidation of emotional declarative memory. Psychol. Sci. 17 (10), 891–898.
 Kaida, K., Takahashi, M., Åkerstedt, T., Nakata, A., Otsuka, Y., Haratani, T., Fukasawa,
- K., 2006. Validation of the Karolinska sleepiness scale against performance and EEG variables. Clin. Neurophysiol. 117 (7), 1574-1581.
- Kaida, K., Niki, K., Born, J., 2015. Role of sleep for encoding of emotional memory. Neurobiol. Learn. Mem. 121, 72–79.
- Kensinger, E.A., 2009. Remembering the details: effects of emotion. Emotion Rev. 1 (2), 99-113.
- Kroenke, K., Spitzer, R.L., Williams, J.B., 2001. The phq-9. J. Gen. Int. Med. 16 (9), 606-613.
- Lang, P.J., Bradley, M.M., Cuthbert, B.N., 2005. International Affective Picture System (IAPS): Affective Ratings of Pictures and Instruction Manual. NIMH, Center for the Study of Emotion & Attention, Gainesville (Florida).
- Laux, L., Hock, M., Bergner-Köther, R., Hodapp, V., Renner, K.-H., 2013. Das State-Trait-Angst-Depressions-Inventar: STADI. Hogrefe, Göttingen (Germany).
- Leclercq, Y., Schrouff, J., Noirhomme, Q., Maquet, P., Phillips, C., 2011. FMRI artefact rejection and sleep scoring toolbox. Comput. Intell. Neurosci. 2011, 598206
- Lewis, P., Cairney, S., Manning, L., Critchley, H.D., 2011. The impact of overnight consolidation upon memory for emotional and neutral encoding contexts. Neuropsychologia 49 (9), 2619-2629.
- Luck, D., Leclerc, M.-E., Lepage, M., 2014. The potentiation of associative memory by emotions: an event-related fMRI study. Adv. Neurosci. 2014, 964024
- Marchewka, A., Żurawski, Ł., Jednoróg, K., Grabowska, A., 2014. The Nencki Affective Picture System (NAPS): Introduction to a novel, standardized, wide-range, highquality, realistic picture database. Behav. Res. Methods 46 (2), 596-610.
- Marshall, L., Born, J., 2007. The contribution of sleep to hippocampus-dependent memory consolidation. Trends Cognit. Sci. 11 (10), 442-450.
- Mednick, S.C., McDevitt, E.A., Walsh, J.K., Wamsley, E., Paulus, M., Kanady, J.C. Drummond, S.P., 2013. The critical role of sleep spindles in hippocampal-dependent memory: a pharmacology study. J. Neurosci. 33 (10), 4494–4504. Meltzer, L.J., Hiruma, L.S., Avis, K., Montgomery-Downs, H., Valentin, J., 2015. Comparison of a commercial accelerometer with polysomnography and
- actigraphy in children and adolescents. Sleep 38 (8), 1323-1330.
- Mölle, M., Marshall, L., Gais, S., Born, J., 2002. Grouping of spindle activity during slow oscillations in human non-rapid eye movement sleep. J. Neurosci. 22 (24), 10941-10947
- Mölle, M., Bergmann, T.O., Marshall, L., Born, J., 2011. Fast and slow spindles during the sleep slow oscillation: disparate coalescence and engagement in memory processing. Sleep 34 (10), 1411-1421.
- Moreno-Martínez, F.J., Montoro, P.R., 2012. An ecological alternative to Snodgrass & Vanderwart: 360 high quality colour images with norms for seven psycholinguistic variables. PLoS One 7 (5), e37527.
- Murray, B., Kensinger, E., 2013. A review of the neural and behavioral consequences for unitizing emotional and neutral information. Front. Behav. Neurosci. 7, 42.
- Nishida, M., Pearsall, J., Buckner, R.L., Walker, M.P., 2008. REM sleep, prefrontal theta, and the consolidation of human emotional memory. Cereb. Cortex 19 (5), 1158-1166
- Oldfield, R.C., 1971. The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia 9 (1), 97-113. Ong, J.L., Lo, J.C., Chee, N.I., Santostasi, G., Paller, K.A., Zee, P.C., Chee, M.W., 2016.
- Effects of phase-locked acoustic stimulation during a nap on EEG spectra and declarative memory consolidation. Sleep Med. 20, 88-97
- Payne, J.D., Kensinger, E.A., 2010. Sleep's role in the consolidation of emotional
- episodic memories. Curr. Directions Psychol. Sci. 19 (5), 290–295. Payne, J.D., Kensinger, E.A., 2011. Sleep leads to changes in the emotional memory trace: evidence from fMRI. J. Cognit. Neurosci. 23 (6), 1285–1297.
- Payne, J.D., Stickgold, R., Swanberg, K., Kensinger, E.A., 2008. Sleep preferentially enhances memory for emotional components of scenes. Psychol. Sci. 19 (8), 781–788.
- Payne, J.D., Kensinger, E.A., Wamsley, E.J., Spreng, R.N., Alger, S.E., Gibler, K., Stickgold, R., 2015. Napping and the selective consolidation of negative aspects of scenes, Emotion 15 (2), 176-186.
- Prehn-Kristensen, A., Munz, M., Molzow, I., Wilhelm, I., Wiesner, C.D., Baving, L., 2013. Sleep promotes consolidation of emotional memory in healthy children but not in children with attention-deficit hyperactivity disorder. PLoS One 8 (5), e65098.
- Randler, C., 2013. German version of the reduced Morningness-Eveningness Questionnaire (rMEQ). Biol. Rhythm Res. 44 (5), 730–736.
- Rasch, B., Born, J., 2013. About sleep's role in memory. Physiol. Rev. 93 (2), 681-766.

- Saletin, J.M., Goldstein, A.N., Walker, M.P., 2011. The role of sleep in directed forgetting and remembering of human memories. Cereb. Cortex 21 (11), 2534-2541.
- Schabus, M., Dang-Vu, T.T., Albouy, G., Balteau, E., Boly, M., Carrier, J., Philips, C., 2007. Hemodynamic cerebral correlates of sleep spindles during human non-rapid eye movement sleep. Proc. Natl. Acad. Sci. 104 (32), 13164-13169.
- Schabus, M., Hoedlmoser, K., Pecherstorfer, T., Anderer, P., Gruber, G., Parapatics, S., Zeitlhofer, J., 2008. Interindividual sleep spindle differences and their relation to learning-related enhancements. Brain Res. 1191, 127–135.
- Schelling, D., Schächtele, B., 2001. Visueller und Verbaler Merkfähigkeitstest (VVM). Swets & Zeitlinger B.V., Swets Test Services, Frankfurt (Germany).
- Schmidt, C., Peigneux, P., Muto, V., Schenkel, M., Knoblauch, V., Münch, M., Cajochen, C., 2006. Encoding difficulty promotes postlearning changes in sleep spindle activity during napping. J. Neurosci. 26 (35), 8976–8982. Schönauer, M., Grätsch, M., Gais, S., 2015. Evidence for two distinct sleep-related
- long-term memory consolidation processes. Cortex 63, 68-78.
- Snodgrass, J.G., Corwin, J., 1988. Pragmatics of measuring recognition memory: applications to dementia and amnesia. J. Exp. Psychol. Gen. 117 (1), 34-50.
- Sopp, M.R., Michael, T., Weeß, H.-G., Mecklinger, A., 2017. The role of right-dominant prefrontal theta oscillations during REM-sleep in the consolidation of emotional episodic memories. Cognit. Affect. Behav. Neurosci. 17 (6), 1186-1209.
- Stickgold, R., Walker, M.P., 2013. Sleep-dependent memory triage: evolving generalization through selective processing. Nat. Neurosci. 16 (2), 139-145.
- Studte, S., Bridger, E., Mecklinger, A., 2015. Nap sleep preserves associative but not item memory performance. Neurobiol. Learn. Mem. 120, 84-93.

- Studte, S., Bridger, E., Mecklinger, A., 2017. Sleep spindles during a nap correlate with post sleep memory performance for highly rewarded word-pairs. Brain Lang, 167, 28-35.
- Talamini, L.M., Nieuwenhuis, I.L., Takashima, A., Jensen, O., 2008. Sleep directly following learning benefits consolidation of spatial associative memory. Learn. Mem. 15 (4), 233-237.
- Tucker, M.A., Tang, S.X., Uzoh, A., Morgan, A., Stickgold, R., 2011. To sleep, to strive,
- or both: how best to optimize memory. PLoS One 6 (7), e21737. Van Der Helm, E., Gujar, N., Nishida, M., Walker, M.P., 2011. Sleep-dependent facilitation of episodic memory details. PLoS One 6 (11), e27421.
- Ventura-Bort, C., Low, A., Wendt, J., Molto, J., Poy, R., Dolcos, F., Weymar, M., 2016. Binding neutral information to emotional contexts: brain dynamics of long-term recognition memory. Cognit. Affect. Behav. Neurosci. 16 (2), 234-247
- Vorster, A.P., Born, J., 2015. Sleep and memory in mammals, birds and invertebrates. Neurosci. Biobehav. Rev. 50, 103-119.
- Walker, M.P., van der Helm, E., 2009. Overnight therapy? The role of sleep in emotional brain processing. Psychol. Bull. 135 (5), 731-748.
- Wiesner, C.D., Pulst, J., Krause, F., Elsner, M., Baving, L., Pedersen, A., Göder, R., 2015. The effect of selective REM-sleep deprivation on the consolidation and affective evaluation of emotional memories. Neurobiol. Learn. Mem. 122, 131-141.
- Wilhelm, I., Diekelmann, S., Molzow, I., Ayoub, A., Mölle, M., Born, J., 2011. Sleep selectively enhances memory expected to be of future relevance. J. Neurosci. 31 (5), 1563–1569.
- Yonelinas, A.P., 2002. The nature of recollection and familiarity: a review of 30 years of research. J. Mem. Lang. 46 (3), 441-517.