Alpha Oscillatory Activity Prior to Encoding Modulates Memory Consolidation during Wake but not Sleep

Zachariah R. Cross[1], Amanda Santamaria[1], Andrew W. Corcoran[1, 2], Phillip M. Alday[1, 3], Scott Coussens[1], Mark J. Kohler[1]*

[1]Centre for Cognitive and Systems Neuroscience, University of South Australia, Adelaide, Australia.
[2]Cognition and Philosophy Laboratory, Monash University, Melbourne, Australia.
[3]Max Planck Institute for Psycholinguistics, Nijmegen, 6500 AH, The Netherlands.

*Corresponding author: Tel. +61 8 8302 4919, e-mail: mark.kohler@unisa.edu.au

ABSTRACT: Sleep promotes memory consolidation through unique neuromodulatory activity. However, little is known about the impact of attention during pre-sleep memory encoding on later memory performance. The current study aimed to address the question of whether attentional state prior to encoding, as indexed by alpha oscillatory activity, modulates the consolidation of images across periods of sleep and wake. 22 participants aged 18 – 41 years (mean age = 27.3) viewed 120 emotionally valenced images (positive, negative, neutral) before a 2hr afternoon sleep opportunity and an equivalent period of wake. Following the sleep and wake conditions, participants were required to distinguish between 120 previously seen (target) images and 120 new (distractor) images. Relative alpha power – adjusted according to participants' individual alpha frequency – was computed to index attentional state prior to the learning phase. Generalised linear mixed effects modelling revealed memory performance was modulated by attention, such that greater pre-encoding alpha synchronisation promoted memory consolidation after wake, but not sleep. There was no difference in memory performance between positive, negative and neutral stimuli. Modulations in alpha oscillatory activity may help coordinate the flow of information between task-relevant cortical regions and a thalamo-cortical loop that subserves the formation of memory during times of wake but not sleep.

Keywords: Attention; Sleep; Memory Consolidation; Neuronal Oscillations; Individual Alpha Frequency

1. Introduction

Due to the limited processing capacity of the central nervous system, emotional information is often prioritised over neutral information. This prioritisation of emotional information modulates memory across encoding, consolidation and retrieval (LaBar & Cabeza, 2006). Encoding is the acquisition of new information in newly constructed representations, while consolidation transforms these representations into stable forms, integrating them into existing knowledge networks, which are then accessible during retrieval (Diekelmann, Wilhelm & Born, 2009). Behavioural (Kensinger, Garoff-Eaton & Schacter, 2007) and neuroimaging (Uribe, Garcia & Tomaz, 2011) studies of emotional memory also reveal that attention (Brenner, Rumak, Burns & Kieffaber, 2014; Maddox, Naveh-Benjamin, Old & Kilb, 2012) and sleep (Groch, Wilhelm, Diekelmann & Born, 2013) are important modulators at encoding and consolidation. At encoding, attention is preferentially allocated to emotional over neutral information, facilitating enhanced consolidation of emotional information (Vuilleumier, 2005). Similarly, it has been suggested that sleep provides a suitable environment for unique neuromodulatory processes to facilitate the distribution of hippocampally-dependent information into neocortical long-term memory (LTM) networks (Ellenbogen, Hulbert, Stickgold, Dinges & Thompson-Schill, 2006). However, little is known regarding the interactive effect of attention and sleep on the emotional modulation of LTM.

1.1. Impact of attention on emotional memory

Emotional content influences attention during encoding (Barnacle, Montaldi, Talmi & Sommer, 2016). Regions of the brain activated by emotional content, such as the amygdala, promote hippocampal-dependent memory consolidation (LaBar & Cabeza, 2006; Murty, Ritchey, Adcock & LaBar, 2010; Smith, Henson, Dolan & Rugg, 2004). Similarly, behavioural studies have demonstrated greater attention is paid to emotional compared to neutral content within divided attention tasks, resulting in superior memory for emotional over neutral stimuli at delayed recall intervals (Maddox et al., 2012; Sakaki, Niki & Mather, 2012).

Given the high temporal resolution of electroencephalography (EEG), event related potentials (ERP) are useful in assessing the time course of neural activation patterns of attention to emotional stimuli (for review: Schupp, Flaisch, Stockburger & Junghofer, 2006). However, ERPs are limited in their representation of the neural mechanisms that underpin fluctuations in attention. The excitation of cortical structures may be mediated by more rhythmic activity over extended periods of time, reflecting the organisation and interconnectivity of attentional networks (Payne & Sekular, 2014; Pfurtscheller, Stancak & Neuper, 1996; Yordanova, Kolev & Polich, 2001). High amplitude, low frequency oscillations occurring in the alpha-band (~8 – 12 Hz) are believed to index coherent activity in attentional networks (Güntekin & Başar, 2014; Klimesch, 2012; Uusberg, Uibo, Kreegipuu & Allik, 2013).

Alpha desynchronisation (i.e. decrease in amplitude) is viewed as reflecting the activation of cortical areas with increased neuronal excitability, whereas alpha synchronisation (i.e. increase in amplitude) reflects the inhibition of brain regions (Klimesch, 2012). This inhibitory account of alpha is supported by a series of recent studies (for review: Sadaghiani & Kleinschmidt, 2016), and highlights the need to move beyond the view that alpha simply

reflects passive neural idling (cf. Pfurtscheller et al., 1996). For example, Sadaghiani and Kleinschmidt (2016) posit that the regulation of alpha power occurs via a cingulo-opercular network, while dorsal fronto-parietal regions downscale alpha power via a top-down influence on local, task-relevant regions. In support of this view, Walz and colleagues (2015) reported an association between greater alpha desynchronisation and the activation of brain regions involved in attentional processing (i.e., bilateral thalamus and posterior parietal cortex) with enhanced behavioural performance on an auditory oddball task. These findings support proposals (e.g. Hanslymayr et al., 2011; Klimesch, 2012; Klimesch, Sauseng & Hanslmayr, 2007) that alpha oscillations gate the flow of information in cortico-thalamic and intra-cortical circuits, and in turn, shape attention and perception.

Uusberg et al. (2013) tested this hypothesis by measuring alpha activity while subjects viewed emotionally valenced stimuli, and reported increased alpha-band event-related desynchronisation (ERD) in response to aversive compared to neutral stimuli. Analogous research corroborates this finding, suggesting alpha ERD to emotional information reflects enhanced neuronal inhibition induced by affective attention, whereby attention is focused on emotional stimuli for heightened sensory processing (Aftanas et al., 2002; Güntekin & Başar, 2007; Onoda et al., 2007). This interpretation is consistent with behavioural findings of valence-induced changes in attention at encoding and superior performance for emotional stimuli at recall (Riggs, McQuiggan, Farb, Anderson & Ryan, 2011).

1.2. Attention in sleep-dependent emotional memory

Evidence suggests typical nocturnal sleep or daytime naps facilitate memory formation compared to wakefulness (Born & Wilhelm, 2012; Mednick Nakayama & Stickgold, 2003; Wagner, Gais & Born, 2001), and particularly for emotional memories (Diekelmann et al., 2009; Groch et al., 2013; Hutchison & Rathore, 2015; Payne et al., 2015). Studies investigating the relationship between sleep and emotional memory consolidation have not accounted for attention during encoding, limiting the ability to establish links between attention-related memory enhancement and sleep-dependent memory consolidation. This limitation is emphasised by Saletin & Walker (2012), who argue that sleep-dependent memory consolidation involves a discriminatory mechanism that is determined by salient cues at encoding, such as emotionality, resulting in a prioritisation of emotional over neutral information. As attentional biases toward emotional information lead to enhanced memory performance (MacKay et al., 2004; Riggs et al., 2011), alpha desynchronisation at encoding may serve to modulate emotional memory consolidation (Everaert & Koster, 2015; Smith et al., 2004; Wang & Bastiaansen, 2014). Further, if sleep plays an active role in memory consolidation, and if alpha rhythms reflect modulations in attention and perception, alpha oscillatory activity at encoding should further modulate memory performance after a period of sleep compared to an equivalent period of wake.

The present study examined whether attention modulates memory consolidation for emotional information across a period of sleep versus wakefulness. Specifically, this study aimed to determine whether individual alpha oscillatory activity at encoding facilitates sleep-dependent memory consolidation and whether this facilitation is higher for emotional compared to neutral stimuli.

2. Method

2.1. Participants

Participants included 22 right-handed healthy adults (10 male) ranging from 18 – 41 years old (mean age = 27.3). Power analyses using G*Power 3 (Faul, Erdfelder, Lang & Buchner, 2007) of previous studies examining the impact of attention on memory (Herbert et al., 2008) and impact of sleep on emotional memory (Payne et al., 2008) suggested a sample size of 12 would be adequate to detect similar sized effects in a repeated measures design (β=.80, α=.05). All participants reported normal or corrected-to-normal vision and hearing and had no current or past psychiatric conditions, substance dependence or abuse, intellectual impairment and were not taking medication that influenced sleep and neuropsychological measures. All participants provided informed consent and received a $40 honorarium. One participant did not return during the second condition, resulting in a final sample size of 21 (9 males; mean age = 26; age range = 18 – 41). Ethics for this study was granted by the University of South Australia's Human Research Ethics committee (I.D: 0000032556).

2.2. Design

This study was a repeated measures within-subjects experimental design with two conditions (sleep, wake). Each condition was counterbalanced across participants and separated by one week to control for condition order effects and to avoid interference between task sets. Conditions included:

a) Sleep condition: Participants underwent learning with an immediate retrieval task followed by a 2hr sleep opportunity. A delayed retrieval task occurred thirty minutes after waking.

b) Wake condition: Participants underwent learning with an immediate retrieval task. This was followed by a delayed retrieval task after a 2hr wake period.

2.3. Materials and measures

2.3.1. Demographic measures

Participants completed a paper questionnaire containing questions on age, sex, ethnicity, highest level of education achieved and recent (<24hr) alcohol and caffeine consumption, as caffeine and alcohol are known to influence performance on cognitive tasks (Keenan, Tiplady, Priestley & Rogers, 2014).

2.3.2. Screening measures

The Pittsburgh Sleep Quality Index (PSQI; Buysse, Reynolds, Monk, Berman & Kupfer, 1989) was used to screen for sleep quality. Participants' PSQI scores ranged from 1 – 5 (M = 3.4, SD = 1.50), indicating good sleep quality. The WASI-II was used to ensure average intellectual ability, as intelligence may influence memory retention and performance on memory tasks (Conway, Kane & Engle, 2003). The WASI-II provides an estimate of full-scale IQ (FSIQ). Participants' mean FSQI score was 114 (SD = 16.44), placing participants in a high range of intellectual functioning (Wechsler, 2011).

2.3.3. Polysomnography (PSG)

PSG was recorded using the Compumedics Grael High-Definition PSG 24-bit amplifier (Compumedics Pty Ltd., Melbourne, Australia). Electrodes were arranged according to the International 10-20 System (American Electroencephalographic Society, 1994) at the following locations: FP1, FP2, F3, F4, C3, C4, T7, T8, P3, P4, P7, P8, O1, O2. In addition to left and right electro-oculography (EOG), sub-mental electromyography (EMG) and electrocardiography (ECG), EEG was recorded and referenced to contralateral mastoids and sampled at a rate of 512 Hz with a bandpass filter from DC to 143 Hz. All impedances were kept at or below 10kΩ throughout recording periods. All sleep data were scored by an experienced sleep technician according to standardised criteria (Berry et al., 2012) with EEG viewed with a high pass filter of 0.3 Hz and a low pass filter of 35 Hz. The following sleep parameters were derived from PSG recordings: time in bed, total sleep time (TST), sleep onset latency (SOL; time from lights out to the first epoch of sleep), REM onset latency, sleep efficiency (SE) [(total sleep time/time in bed) x 100], wake after sleep onset, total arousal index, duration and percent of TST spent in each sleep stage.

2.4. EEG paradigm (attentional state)

EEG was continuously recorded during a visual Conjunctive Continuous Performance Task (CCPT-V), which was used to elicit sustained attention derived from target discrimination in the visual modality. The CCPT-V began with 15 practice trials followed by 320 trials and took approximately eight minutes to complete (Shalev, Ben-Simon, Mevorach, Cohen & Tsal, 2011). Stimuli were coloured geometric shapes and were presented in the centre of a computer monitor. Target probability (red square) was 30%, non-red square probability was 17.5% and all other shape (neither a square nor red) probability was 35%. Each inter-stimulus interval (ISI) appeared in 25% of trials and both the stimuli and ISIs were randomly selected (Shalev et al., 2011). Participants were instructed to press a key on a standard keyboard whenever a target appeared and to refrain from responding to all other stimuli. An example stimulus train is presented in Figure 1.

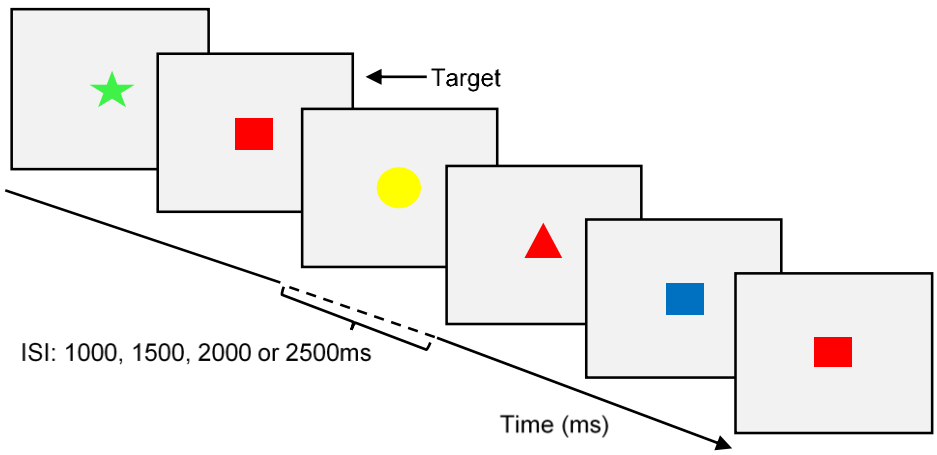

Figure 1. Example of a sequence of trials on the Conjunctive Continuous Performance Task – Visual. Stimulus presentation was 100ms, separated by an ISI of 1000, 1500, 2000 or 2500ms.

2.5. Memory task

480 pictures were used from the International Affective Picture System (IAPS; Lang, Bradley & Cuthbert, 2008), which were divided into two parallel sets (Set A, Set B), counterbalanced across the sleep and wake conditions. The IAPS are rated for emotionality based on two dimensions (valence: 1=unpleasant, 9=pleasant; arousal: 1=calm, 9=excited) by a normative adult sample (Lang et al., 2008). Mean valence and arousal ratings of the stimuli have high internal consistency (*a*=.94) and split-half reliability (*r*s=.94).

Stimuli were displayed via OpenSesame Software version 2.9.7 (Mathôt, Schreij & Theeuwes, 2012) and were categorised into three groups (i.e., negative, neutral, positive) according to their mean valence values. Negative pictures had a mean valence rating of 3.27 (*SD* = 0.03), neutral pictures had a mean valence rating of 5.02 (*SD* = 0.03), and positive pictures had a mean valence rating of 7.00 (*SD* = 0.03). All stimuli were counterbalanced based on valence and arousal.

During the learning tasks, 120 stimuli, each containing 40 neutral, 40 positive and 40 negatively valenced images, were presented sequentially for participants to learn, followed by an immediate retrieval task to gain a recognition baseline. A delayed retrieval task occurred post experimental conditions. The immediate and delayed retrieval tasks contained 120 previously seen pictures intermixed with 120 new (distractor) pictures (see Figure 2 for schematic representation). Following presentation, participants judged whether pictures were old or new. Pictures were pseudo-randomised at each time of testing, such that no more than two pictures of the same emotion followed. Testing time for each experimental task was approximately 20 – 30 minutes.

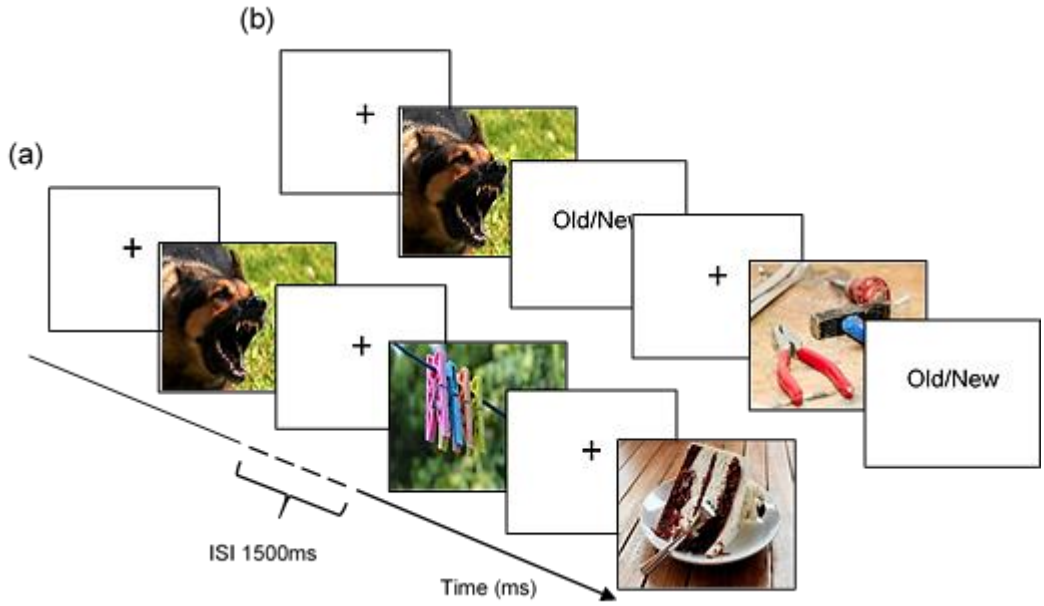

Figure 2. (a) Schematic representation of the learning task. Stimuli were presented for 1000ms to allow for conscious processing whilst maintaining an appropriate degree of difficulty. Each stimulus was preceded by a 500ms fixation cross with a temporal jitter of ± 100ms and with an ISI of 1500ms; (b) Schematic representation of the retrieval task. Stimuli were presented until

button press with a timeout at 5000ms, preceded by a 500ms fixation cross with a jitter of ± 100ms. Participants then indicated whether the stimulus was old or new. Images are taken from Creative Commons for illustrative purposes, as the IAPS are protected from the public.

2.6. Procedure

Participants came to the laboratory at approximately 11:45hr, and were taken through to the testing rooms for PSG/EEG set-up. Baseline EEG activity was recorded during quiet sitting with eyes open (focussing on a fixation cross centred on a computer monitor) and eyes closed for two minutes, respectively. Participants then completed the CCPT-V and learning task by approximately 13:30hr, followed by the immediate recall task.

During the wake condition, participants were administered the WASI-II and engaged in non-strenuous activity (e.g., reading). During the sleep condition, participants were given a 120-minute sleep opportunity between the hours of 14:30hr and 16.30hr. Nap success rate was 100%. PSG data was used to verify sleep periods. Participants engaged in non-strenuous activity for 30 minutes after the nap until testing to alleviate inertia effects on memory performance (Cairney, Durrant, Hulleman & Lewis, 2014; Payne et al., 2008; Tassi & Muzet, 2000). At approximately 17:00hr, participants completed the delayed retrieval task (see Figure 3 for study protocol).

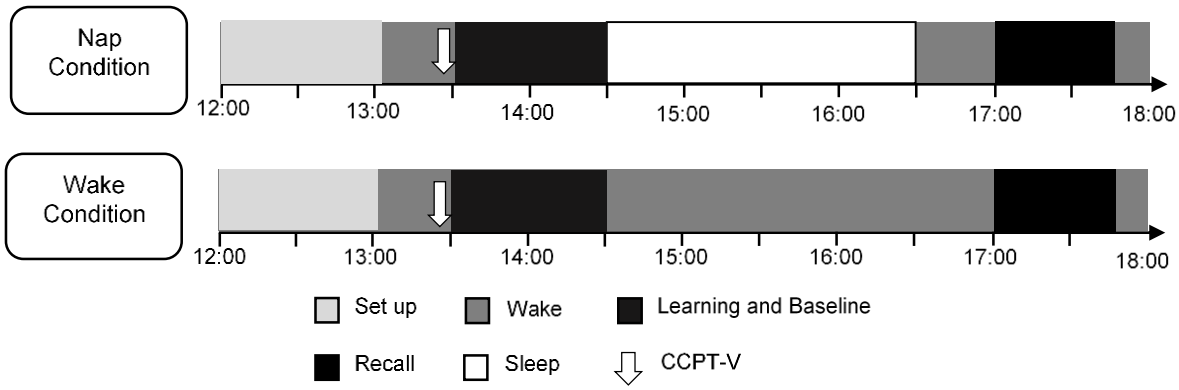

Figure 3. Diagram representing the time course of the experimental conditions (sleep, wake) and testing session (learning, retrieval). Timing of the CCPT-V is shown in downward arrows at approximately 13.25hr.

3. Data Analysis

3.1. Behavioural data

The mean response time (ms) to correct responses (M-RT), the percentage of commission errors, and percentage of correct responses were determined from CCPT-V performance. M-RT reflects response time, while commissions and the percentage of correct responses reflect aspects of the accuracy of responses (Shalev et al., 2011). Memory performance was calculated on a trial-by-trial basis, determined by whether participants correctly identified target and distractor stimuli.

3.2. EEG pre-processing and spectral analysis

All EEG analysis procedures were conducted using customised scripts programmed in MATLAB® (R2015a, The MathWorks, Inc., Natick, MA, USA). EOG and parieto-occipital EEG channels (P3-M2, P4-M1, O1-M2, and O2-M1) were imported into MATLAB via the EEGLAB toolbox (v13.6.5b; Delorme & Makeig, 2004) and subjected to zero-phase, finite impulse response highpass (passband edge: 1 Hz, -6 dB cutoff: 0.5 Hz) and lowpass (passband edge: 40 Hz, -6 dB cutoff: 45 Hz) Hamming-windowed sinc filters (implemented via the pop_eegfiltnew function of the firfilt plugin; v1.6.1). Datasets were then divided into two separate segments corresponding to the eyes-closed resting-state and CCPT-V portions of the EEG recording. An automated artifact detection routine was applied to both segments in order to exclude blinks and other sources of signal contamination. The peak-to-peak threshold for artifact rejection was set at +/- 75 µV, and applied within a 500ms sliding window (50% overlap). EOG channels were removed from the data following artifact rejection.

One-sided PSD estimates were generated via the MATLAB implementation of Welch's modified periodogram method (Welch, 1967). This technique divides the signal into equal segments, multiplies each segment by a tapering window of identical length, computes the fast Fourier transform of this product, and averages across the resulting periodograms to estimate the PSD. We applied a 2048 sample (4s) Hamming window with 50% overlap across segments, yielding a frequency resolution of 0.25 Hz. For each channel, PSD estimates were normalised by dividing each power estimate within the passband by the mean of these estimates. This step was designed to facilitate comparison of spectral activity across conditions.

Channel-wise PSD estimates derived over the duration of the CCPT-V task were averaged for each participant, and summed across alpha-band frequency bins to summarise the quantity of alpha-band activity per condition. Alpha bandwidth was defined as 2 Hz above and below the participant's individual alpha frequency (IAF). Two indices of IAF (peak frequency and centre of gravity) were calculated from eyes-closed resting-state recordings (estimates from the sleep and wake conditions were averaged). IAF estimates were obtained using *restingIAF* v1.0, an open-source package available from https://github.com/corcorana/restingIAF. This routine searches the first derivative of the smoothed PSD for evidence of peak activity within a defined frequency interval (here, 7–13 Hz), and parameterises the bounds of identified peak components to compute their centre of gravity. The minimum number of channels required to estimate IAF was set to 1 due to the low number of channels available for analysis. All other analysis parameters were as per default settings (see Corcoran, Alday, Schlesewsky, & Bornkessel-Schlesewsky, 2017).

3.3. Statistical analysis

Data were entered into *R* version 3.4.0 (*R* Core Team, 2017) for Windows, and the *lme4* package for linear mixed-effects models (Bates, Maechler, Bolker & Walker, 2015). A generalised linear mixed effects model (GLMM) with a logit link function fit by maximum likelihood was used to examine the relationship between alpha oscillatory activity, emotional valence and sleep on memory consolidation.

Mixed models are an appropriate method for analysing data from repeated measure designs, as these designs are grouped by subject and appropriately account for within and between subject variance (Judd, Westfall & Kenny, 2012; Van Dongen, Olofsen, Dinges & Maislin, 2004). Further, logit mixed models appropriately account for binomial response variables (Jaeger, 2008). As such, a logit mixed model is particularly suited to the current data due to: (a) large inter-individual differences in IAF estimates; (b) inter-individual differences in response to the emotional valence of each stimulus, and; (c) the use of categorical response variables (i.e., binomial old/new memory responses) as a measure of memory performance.

Condition (sleep, wake), Valence (positive, negative, neutral) and Alpha were specified as fixed effects. Alpha power was centred via a z-transformation prior to inclusion in the GLMM. The model included random-effects terms for items and participant on the intercept. Memory performance (correct-by-trial) was specified as the dependent variable. Inspection of the residual plots for the mixed models revealed no deviations from normality or homoscedasticity. Akaike Information Criterion (AIC; Akaike, 1974), Bayesian Information Criterion (BIC; Schwarz, 1978) and log-likelihood were used to assess the fit of the GLMM. All models were fully saturated with main and interaction effects for Condition, Valence and Alpha, while Type II Wald Chi-Square ($\chi 2$) tests from the *car* package in *R* (Fox & Weisberg, 2011) were used to provide *p*-value estimates for each of the factors. All *p*-values are 2-tailed, with statistical significance determined at $\alpha = 0.05$. All data are presented as mean and standard deviation (SD) unless indicated otherwise, and effects were plotted using the package *effects* (Fox, 2003) and ggplot2 (Wickham, 2009).

4. Results

4.1. Preliminary analyses

Preliminary analyses were conducted to: (1) determine if there were any differences in behavioural performance on the CCPT-V measures between conditions; (2) determine the sleep characteristics of the nap; (3) determine if there were any differences in alpha power between the two conditions, and; (4) determine if the behavioural measure of sustained attention derived from the CCPT-V produces an equivalent effect on memory as alpha power. Since the IAF estimators were highly correlated ($r = .96$, $p < .001$, 95% CI = [.90, .98]), all reported alpha power estimates were derived from individual bandwidths centred on the peak alpha frequency (see supplementary materials for reanalysis of power estimates in relation to the alpha centre of gravity). Peak alpha frequency estimates from both conditions are displayed in Figure 4.

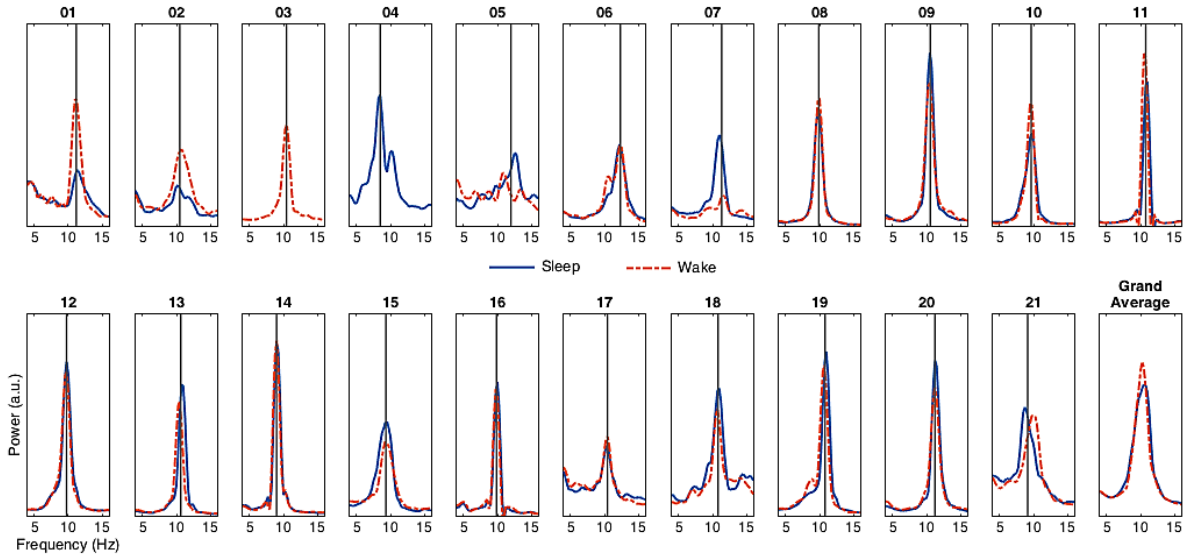

Figure 4. Individual (peak) alpha frequency (IAF) estimates from eyes-closed resting-state recordings prior to the Sleep (blue, solid lines) and Wake (red, broken lines) conditions. Vertical line indicates the mean IAF estimate used to locate the individualised alpha bandwidth for the main analysis. Note that resting-state data were missing for participant 4 during the Wake condition. Participant 3 did not demonstrate evidence of a distinct alpha peak during the Sleep condition resting-state recording, hence IAF is estimated on the basis of the Wake condition peak frequency. a.u.: arbitrary units.

Paired sample *t*-tests conducted between the three CCPT-V performance measures demonstrated no significant difference between conditions in reaction times ($t(20)=.36$, $p=.72$), percentage of commissions ($t(20)=.60$, $p=.60$) and percentage of correct responses ($t(20)=.67$, $p=.50$). See Table 1 for means and standard deviations of the CCPT-V performance measures. Similarly, paired samples *t*-test indicated relative alpha power did not differ between the sleep ($M=30.81$, $SD=17$) and wake ($M=28.31$, $SD=16.16$) conditions ($t(20)=.92$, $p=.36$).

Table 1.

Means and Standard Deviations of Reaction Times, the Percentage of Commissions and the Percentage of Correct Responses for the CCPT-V between the Sleep and Wake Conditions.

CCPT-V Variables	Condition	
	Sleep M (SD)	Wake M (SD)
Reaction Time (ms)	422.35 (39.11)	419.14 (41.92)
% of Commissions	0.74 (0.51)	0.81 (0.65)
% of Correct Responses	99.55 (1.02)	99.21 (2.02)

Sleep variables of total sleep time, sleep onset latency, wake after sleep onset and the amount of time and percentage of sleep spent in stage 1 (N1), stage 2 (N2), SWS and REM are reported in Table 2. Sleep data show the expected proportion of NREM sleep stages (i.e., N1,

N2 and SWS) and minimal REM sleep (Payne et al., 2015). That is, although 81 percent of participants experienced REM, average time spent in this stage was 10 minutes (SD = 7.71).

Table 2.

Means, Standard Errors and Ranges for Sleep Parameters.

Sleep Parameters	Minutes	
	Mean (SEM)	Range
TST (min)	91.45 (5.76)	23 – 119
SOL (min)	13.64 (3.07)	1 – 53.5
WASO (min)	15.10 (3.86)	2.5 – 65.5
N1 (%TST)	7.07 (1.23)	0.5 – 20.5
N2 (%TST)	46.76 (3.76)	16.5 – 73.5
SWS (%TST)	29.04 (3.61)	0 – 61.5
REM (%TST)	8.57 (1.78)	0 – 36.5

Note. SEM = standard error of the mean. TST = total sleep time; SOL = sleep onset latency; WASO = wake after sleep onset; N1 = stage 1; N2 = stage 2; SWS = slow wave sleep; REM = rapid eye movement sleep; min = minutes.

4.1.1. CCPT-V and memory

A GLMM was computed with CCPT-V (percentage of correct responses), Valence (positive, negative, neutral) and Condition (sleep, wake) as fixed effects and random intercepts by participant and by stimulus as random effects. Memory performance (correct-by-trial) was specified as the dependent variable (see Table 3 for a model summary). This analysis was conducted to determine if a behavioural measure of attention prior to encoding modulates memory performance across the sleep and wake conditions. While there was no effect of Condition ($\chi2(1)=3.20$, $p=.07$), there was a significant effect of CCPT-V ($\chi2(1)=4.97$, $p=.02$) and a significant Condition x CCPT-V interaction ($\chi2(1)=5.30$, $p=.02$), indicating that a 2hr sleep opportunity preserved memory that was encoded under low attentional state relative to an equivalent period of wake (see Figure 5).

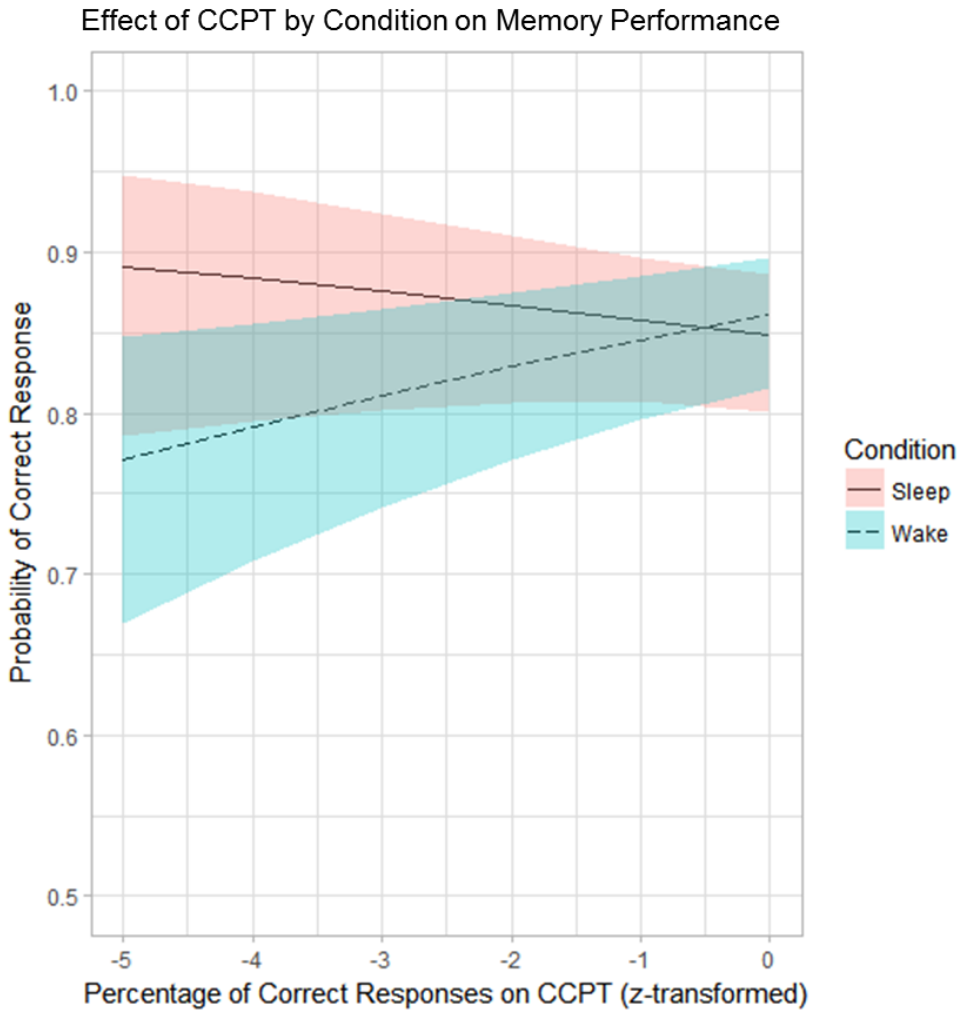

Figure 5. Interaction between percent of correct responses on the CCPT-V and the sleep (red) and wake (blue) conditions on memory performance at delayed recall. Higher values on the y-axis indicate greater memory performance, while higher values on the x-axis indicate greater CCPT-V performance. Please note that since there was no difference in memory performance between the positive, neutral and negative stimuli, stimuli were collapsed stimuli across each valence to provide an overall measure of memory performance (the *marginal* effect of memory performance). The blue and red shaded space indicate the 95% confidence interval.

Table 3.

Generalised Linear Mixed Model Fit by Maximum Likelihood (Laplace Approximation) with Percentage of Correct Responses on the CCPT as a Behavioural Measure of Attentional State Prior to Encoding.

	AIC	BIC	LogLik	Deviance
	9016.3	9117.4	-4494.2	8988.3
Scaled residuals:				
Min	IQ	Median	3Q	Max
-7.43	0.20	0.35	0.48	2.59
Random effects:				
Groups	Name	Variance	SD	
Stimulus ID	(Intercept)	0.64	0.80	
Participant	(Intercept)	0.54	0.73	
Residual				
Number of Observations: 10061, groups: Stimulus, 480; Subject, 21.				
Fixed effects				
	Estimate	Std. Error	t value	
(Intercept)	1.77	0.16	10.52	
Valence (Neg)	-0.12	0.06	-1.85	
Valence (Pos)	-0.00	0.06	-0.02	
Condition	0.04	0.02	1.81	
CCPT	0.02	0.04	0.57	
Valence (Neg) > Condition	0.02	0.03	0.78	
Valence (Pos) > Condition	0.02	0.03	0.54	
Valence (Neg) > CCPT	-0.03	0.04	-0.83	
Valence (Pos) > CCPT	0.01	0.04	0.28	
Condition > CCPT	0.09	0.04	2.29	
Valence (Neg) > Condition > CCPT	0.04	0.04	1.0	
Valence (Pos) > Condition > CCPT	-0.01	0.04	-0.3	

Note: CCPT = Conjunctive Continuous Performance Task; AIC = Akaike Information Criterion; BIC = Bayesian Information Criterion; Min = minimum; Neg = negatively valenced stimuli; Pos = positively valenced stimuli; Std. Error = standard error.

4.2. Primary analysis

All significant effects and interactions of the GLMM of memory performance of correct-by-trial are given in Table 4. Importantly, the model with Alpha yielded the best model fit (see Table 5 for a model summary) compared to the model with CCPT-V as the variable of attentional state. Furthermore, GLMM results indicate a significant effect of Condition, with factor level contrasts revealing memory performance was significantly greater after wake compared to sleep. There was no effect of Valence, translating into a statistically insignificant difference in memory performance between negative, neutral and positive stimuli. Finally, a significant effect of Alpha was indicated for memory performance, such that enhanced memory performance was predicted by increased alpha power at encoding.

Table 4.

Inferential Statistics for all Main Effects and Interactions with Chi-Square ratio values, Degrees of Freedom and Statistical Significance. Final Column Display Significant Factor Level Contrasts.

Effect	χ^2	*df*	*p*	Contrasts
Condition	6.85	1	.008	Wake > Sleep
Valence	4.65	2	.09	
Alpha	12.93	1	<.001	
Condition x Valence	1.68	2	.43	
Valence x Alpha	0.90	2	.63	
Condition x Alpha	24.47	1	<.001	Wake > Sleep
Condition x Valence x Alpha	2.66	2	.26	

There was a significant Alpha x Condition interaction. Factor level contrasts revealed Alpha modulated memory performance greater in the wake compared to the sleep condition, such that memory performance after a period of wake was enhanced with increased alpha power at encoding (see Figure 6). The Condition x Valence interaction was nonsignificant, indicating memory for negative, neutral and positive stimuli did not differ between the sleep and wake conditions. Similarly, the Valence x Alpha interaction was nonsignificant, suggesting enhanced baseline attention did not modulate memory for negative, neutral and positive stimuli. Finally, the Condition x Alpha x Valence interaction was nonsignificant, suggesting alpha power at encoding did not modulate memory performance for negative, neutral or positive stimuli across the sleep and wake conditions.

Table 5.

Generalised Linear Mixed Model Fit by Maximum Likelihood (Laplace Approximation) with Alpha as a Neurophysiological Measure of Attentional State Prior to Encoding.

	AIC	BIC	LogLik	Deviance
	8986.4	9087.4	-4479.2	8958.4
Scaled residuals:				
Min	IQ	Median	3Q	Max
-7.60	0.19	0.35	0.48	2.97
Random effects:				
Groups	Name	Variance	SD	
Stimulus ID	(Intercept)	0.64	0.80	
Participant	(Intercept)	0.69	0.83	
Residual				
Number of Observations: 10061, groups: Stimulus, 480; Subject, 21.				
Fixed effects				
	Estimate	Std. Error	t value	
(Intercept)	1.78	0.18	9.45	
Valence (Neg)	-0.12	0.06	-1.97	
Valence (Pos)	-0.00	0.06	-0.05	
Condition	0.07	0.02	2.65	
Alpha	0.34	0.08	4.17	
Valence (Neg) > Condition	0.02	0.03	0.68	
Valence (Pos) > Condition	0.02	0.03	0.65	
Valence (Neg) > Alpha	-0.03	0.03	-0.93	
Valence (Pos) > Alpha	0.02	0.03	0.78	
Condition > Alpha	0.14	0.02	5.01	
Valence (Neg) > Condition > Alpha	-0.04	0.03	-1.22	
Valence (Pos) > Condition > Alpha	-0.01	0.03	-0.36	

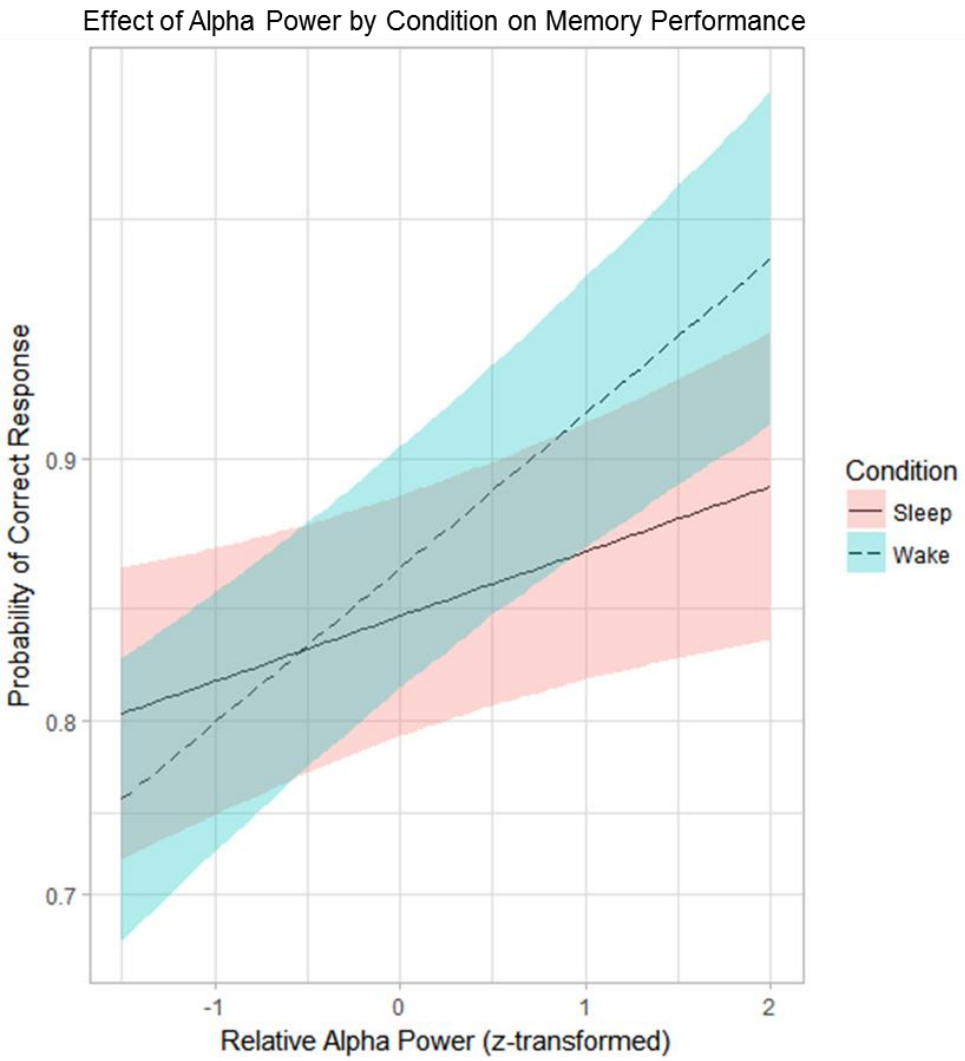

Figure 6. Interaction between relative alpha power and the sleep (red) and wake (blue) conditions on memory performance at delayed recall. Higher values on the y-axis indicate greater memory performance, while higher values on the x-axis indicate greater alpha synchronisation over left (O1-P3) and right (O2-P4) occipital-parietal electrodes during the CCPT-V prior to the learning task. The blue and red shaded space indicate the 95% confidence interval.

5. Discussion

This study aimed to determine whether attentional state prior to encoding influences sleep-dependent memory consolidation for emotionally valenced, compared to neutral stimuli. Contrary to expectations, memory performance was significantly greater after a period of wake than after a 2hr sleep opportunity. Further, emotional valence did not appear to modulate memory, with no difference in memory performance between positive, negative and neutral stimuli. However, results indicated that memory was modulated by attentional state – as indexed by oscillatory alpha activity – and this effect was larger for the wake than the sleep condition. Very few studies have examined the oscillatory correlates of memory encoding prior to a period of sleep (e.g., Heib et al., 2015). We interpret these findings in accordance with the

inhibition-timing hypothesis (Klimesch et al., 2007), and proposals that memory consolidation benefits from the cyclic occurrence of SWS and REM (e.g. Giuditta, 2014).

5.1. Alpha, affective attention and emotional memory

Previous research utilising alpha as an index of attention and cortical inhibition have reported increases in alpha desynchronization to emotional stimuli (Uusberg et al., 2013). This is suggested to reflect a gating mechanism, preferentially processing biologically relevant information, while selectively filtering out less salient information (Aftanas et al., 2002; Uusberg et al., 2013). However, the present study found that enhanced alpha synchronisation prior to encoding resulted in greater memory performance at recall, which is consistent with models that posit alpha synchronisation plays an active role in global neural integration rather than passive neural idling (Basar, Shurmann, Basar-Eroglu & Karakas, 1997; Hanslmayr, Gross, Klimesch & Shapiro, 2011; Klimesch et al., 2007).

According to the inhibition-timing hypothesis (Klimesch et al., 2007), an increase in alpha synchronisation reflects the inhibition of bottom-up processing via attentional mechanisms. As such, the relationship between increased alpha synchronisation and greater memory consolidation might reflect a top-down attentional mechanism for sheltering information from external, task-irrelevant inputs (Hanslmayr et al., 2011). Further, there is strong evidence indicating that increased alpha power regulates the flow of information in the cortex via the synchronised firing of neuronal ensembles in occipital-parietal cortices (Klimesch et al., 2007; Schurmann & Basar, 2001). Cycles of neuronal excitability within these regions may act as a pulsed-inhibition gating mechanism, modulating the flow of task-relevant information to regions further downstream (i.e. entorhinal cortex and regions CA1/CA3) for long-term consolidation (Buzsaki, 1996). This interpretation is in line with evidence demonstrating that the phase of alpha oscillations modulates synaptic spiking, maximising stimulus detection and subsequent mnemonic processing (Canolty & Knight, 2010). For example, Khader and colleagues (2010) reported increased alpha synchronisation while participants engaged in internal mental processing tasks after encoding, which predicted enhanced performance on a delayed recall task. Thus, our findings build on the proposal that alpha oscillations serve as a gating mechanism, modulating memory encoding within a thalamo-neocortical-hippocampal network, opposed to the view that alpha synchronisation merely reflects cortical idling (e.g., Pfurtscheller et. al., 1996).

However, it is important to note the methodological differences between the current study and analogous research on the affective modulation of alpha. Aftanas et al. (2002) and Uusberg et al. (2013) measured event-related spectral perturbations (ERD) in alpha power, finding emotional stimuli to evoke greater alpha ERD than neutral images. While the ERD technique indexes changes in oscillatory activity on a millisecond timescale, it can disregard the importance that the overall brain state has on LTM formation (Hanslmayr, Staudigl & Fellner, 2012). Thus, naturally occurring fluctuations between alpha synchronisation and desynchronisation may promote enhanced cortical processing (Klimesch, 2012; Mathewson et al., 2011; Peterson & Voytek, 2017). This is consistent with our findings, where higher alpha power predicted the consolidation of images, supporting the idea that fluctuations in neuronal excitation promote memory formation (Fell & Axmacher, 2011). Future research indexing

alpha ERD to individual stimuli should also measure rhythmic activity over extended periods of time, as done in this study, which could further elucidate how fluctuations between excitation and inhibition coordinate the formation of hippocampal-dependent memory traces (Hanslmayr et al., 2012).

5.2. Sleep and emotional memory consolidation

Based on research demonstrating a beneficial effect of sleep on memory consolidation generally (Rasch & Born, 2013; Schreiner & Rasch, 2014; Stickgold & Walker, 2013), and a sleep-dependent effect on emotional memory consolidation specifically (Groch et al., 2013; Lewis et al., 2011; Payne, Chambers & Kensinger, 2012; Payne et al., 2015; Wagner et al., 2001), we proposed that memory would be greater after a 2hr nap compared to wake, and that this effect would be accentuated for emotional compared to neutral stimuli. In contrast, memory performance was significantly greater after wake compared to sleep, coupled with no statistically significant difference in memory performance between negative, neutral, and positive stimuli.

Although offering many methodological advantages, such as controlling for circadian effects, an afternoon nap typically lacks REM sleep (Genzel, Spoormaker, Konrad & Dresler, 2015; Payne et al., 2015). As participants in the current study experienced a small amount of REM, memory for neutral and emotional items may have been selectively refined through the synaptic downscaling of SWS (Cairney et al., 2014; Rasch & Born, 2015). Without REM to target neural representations of emotionally valenced items, memory for emotional stimuli may have weakened over time (Nishida, Pearsall, Buckner & Walker, 2009). This interpretation supports studies reporting a beneficial role of REM in promoting emotional plasticity, particularly through theta oscillations (Heib et al., 2015; Hutchison & Rathore, 2015). REM theta oscillations reflect coherent activity between the hippocampus and amygdala and are thought to preferentially strengthen emotionally tagged memory traces (Hutchison & Rathore, 2015). As such, the null effect of sleep reported here may be explained by a lack of REM theta activity, which preferentially strengthens memory traces of emotional stimuli after the synaptic downscaling induced by slow oscillations during NREM sleep (Hutchison & Rathore, 2015).

5.3. Alpha oscillations, sleep and memory consolidation

This study provides preliminary evidence that attention and sleep modulate memory consolidation in distinct ways. Greater attention prior to encoding appears to be important for preserving memory during wakefulness, and that a 2hr sleep opportunity – without sufficient REM – may transiently shelter memory from the external inputs of wakefulness. One possible explanation for the distinction between wake and sleep findings comes from consideration of the interplay of alpha activity with that of theta. Theta rhythms during wake have been associated with enhanced memory formation, wherein after learning emotional stimuli, theta activity has been reported to synchronise between the hippocampus and temporal cortex, reflecting hippocampal-cortical communication (Brenner et al., 2014; Hutchison & Rathore, 2015; Vertes, 2005). During sleep, theta is predominantly evident during REM – a stage limited in the present study by the use of a nap paradigm – which is characterised by an increased production of acetylcholine, an important factor for neuroplasticity (Heib et al., 2015;

(Scheffzuk et al., 2011). During the nap and wake conditions, synchronous alpha activity may have reflected top-down control critical for preventing interference of recently established memory traces, reducing irrelevant information from reaching enhanced processing (Khader et al., 2010; Klimesch et al., 2007). Following encoding, during the wake condition, theta activity may have strengthened memory traces between the hippocampus and amygdala (Heib et al., 2015). However, as the sleep period in this study contained minimal REM, memory traces would be weakened due to the lack of theta activity, leading to poorer memory performance at delayed recall (Hutchison & Rathore, 2015).

The finding that greater pre-encoding alpha synchronisation promoted memory consolidation after wake compared to sleep can be interpreted within the context of the synaptic homeostasis hypothesis (SHY; Tononi & Cirelli, 2014). According to SHY, sleep facilitates the downscaling of synaptic weight accumulated during wake to a baseline level that is homeostatically sustainable, a process performed by slow oscillations during SWS (Mascetti et al., 2013). This process of synaptic renormalisation desaturates the capacity to encode new information during subsequent wake periods by decreasing neuronal excitability, which improves the signal-to-noise ratio in the reactivation of encoded memory traces (Tononi & Cirelli, 2012). It is argued that one function of alpha synchronisation is to prevent competing memory traces from being concurrently activated during memory retrieval (Hanslmayr et al., 2012). From this perspective, the wake condition – having not had the benefits of sleep-based synaptic downscaling – may have required greater internally oriented processing to distinguish between new and old items, as reflected in greater alpha synchronisation. In contrast, the selective downscaling of synaptic weights during sleep in the nap condition may have fine-tuned connections between occipital-parietal cortices and neuronal assemblies further downstream, facilitating quick and efficient memory retrieval.

Taken together, results suggest that theta oscillations – present during wake and markedly increased during REM – may serve complementary roles in the emotional modulation of LTM, and alpha, as a physiological marker of attention and cortical inhibition, may facilitate this process at encoding; however, future research is required to determine the interactive effect that alpha and theta activity have on the emotional modulation of LTM across periods of sleep versus wake. Such research would shed further light on the factors underpinning the attentional modulation of sleep-dependent memory consolidation, which may lead to a greater understanding of disorders in which attentional deficits to emotional information modulate sleep-dependent learning (Baran, Pace-Schott, Ericson & Spencer, 2012). For example, Prehn-Kristensen et al. (2013) found that sleep-facilitated consolidation of emotionally valenced stimuli was impaired in children with attention-deficit-hyperactivity disorder, but not healthy controls, highlighting the role attention may play in sleep and the emotional modulation of LTM.

5.4. Limitations and strengths of current study

As discussed, one major limitation of the current study was minimal REM sleep occurring during daytime naps, as well as large variability in the time participants slept. These effects make it difficult to establish a true effect of sleep. Future research using a nocturnal half-night paradigm would involve presenting participants emotional stimuli before either a

SWS or REM-rich sleep interval (Groch et al., 2013). Nocturnal half-night paradigms account for natural human nocturnal sleep architecture, and would allow for the systematic investigation between alpha activity at encoding and memory consolidation during SWS and REM.

The adoption of a nocturnal half-night paradigm would be complemented by the use of individual valence reports instead of normalised ratings. While the majority of research utilising the IAPS has relied on normalised ratings (Bradley & Lang, 1994; Lang & Bradley, 2007), there may be large inter-individual variability in the way subjects perceive stimuli along the dimensions of valence and arousal (Backs, Silva & Han, 2005). Quantifying emotional memory based on individual self-report ratings may increase model sensitivity and the probability of detecting emotion-enhanced memory effects, similar to previous emotional memory research (for review: Talmi, 2013).

Finally, while averaging alpha power over the course of the CCPT-V enabled quantification of a cortical index of sustained attention, it did not allow for direct observation of event-related changes in the power spectra. While this method yields distinct strengths, it limits the ability to establish links between changes in alpha power at the point of stimulus presentation, making it difficult to infer the relationship between alpha (de)synchronisation and the consolidation of stimulus-specific characteristics. Despite these limitations, the adjustment of the alpha range according to participants' IAF yields greater reliability over utilising the standard 8–12 Hz range. The distribution of alpha-band activity shows substantial variation across individuals, and has been associated with inter-individual differences in information processing and general intelligence (Klimesch, 1997; 1999). Further, anchoring frequency band windows in relation to the IAF as opposed to classically defined bandwidths has been shown to increase sensitivity to band-specific oscillatory dynamics (Doppelmayr, Klimesch, Pachinger, & Ripper, 1998). From this perspective, the effects of alpha reported here are unlikely to be due to overlap with other frequency band activity (e.g. beta, 13–30 Hz; for a discussion on alpha/beta activity and long-term memory, see Hanslmayr et al., 2012).

6. Conclusions

This study demonstrated that attention, as indexed by alpha oscillatory activity, modulates memory consolidation during wake relative to an equivalent period of sleep. These results address a neglected area of research into the sleep-dependent memory consolidation hypothesis: effects of sleep versus wake on the consolidation of various types of memory are often assessed in isolation to memory encoding, limiting the ability to separate encoding-specific factors (e.g. attentional state) from sleep-facilitated consolidation on subsequent memory. From this perspective, alpha oscillatory activity provides a valuable pathway for investigating the neural correlates of attention and sleep-facilitated memory consolidation. However, in line with previous accounts, we posit that REM oscillatory theta activity may underlie post-encoding processes involved in memory consolidation, particularly for emotionally valenced information. Future research should directly measure the combined effect of alpha at encoding, and theta during consolidation, across periods of wake and sleep. This will provide a valuable basis for future research investigating brain mechanisms involved in the interactive effect of attention and sleep on long-term memory consolidation.

Acknowledgements

We thank Professor Ina Bornkessel-Schlesewsky for helpful comments on an earlier version of this manuscript, and Alex Chatburn for valuable discussion. ZRC is supported by a Research Training Program Scholarship awarded by the Australian Commonwealth Government (ID: 212190). The authors declare no competing financial interests.

References

Aftanas, L. I., Varlamov, A. A., Pavlov, S. V., Makhnev, V. P., & Reva, N. V. (2002). Time-dependent cortical asymmetries induced by emotional arousal: EEG analysis of event-related synchronization and desynchronization in individually defined frequency bands. *International Journal of Psychophysiology*, *44*(1), 67-82. doi: 10.1016/S0167-8760(01)00194-5

Akaike, H. (1974). A new look at the statistical model identification. *IEEE transactions on automatic control*, *19*(6), 716-723. doi: 10.1109/TAC.1974.1100705

American Electroencephalographic Society. (1994). Guideline thirteen: Guidelines for standard electrode position nomenclature. *Journal of Clinical Neurophysiology*, *11*, 111-113. Retrieved from http://journals.lww.com/clinicalneurophys/pages/default.aspx

Baran, B., Pace-Schott, E. F., Ericson, C., & Spencer, R. M. (2012). Processing of emotional reactivity and emotional memory over sleep. *Journal of Neuroscience*, *32*(3), 1035-1042. doi: 10.1523/jneurosci.2532-11.2012

Barnacle, G. E., Montaldi, D., Talmi, D., & Sommer, T. (2016). The list-composition effect in memory for emotional and neutral pictures: Differential contribution of ventral and dorsal attention networks to successful encoding. *Neuropsychologia*, *90*, 125-135. doi: 10.1016/j.neuropsychologia.2016.06.023

Basar, E., Schurmann, M., Basar-Eroglu, C., & Karakas, S. (1997). Alpha oscillations in brain functioning: An integrative theory. *International Journal of Psychophysiology*, *26*(1-3), 5-29.

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1-48. doi: 10.18637/jss.v067.i01

Berry, R. B., Brooks, R., Gamaldo, C. E., Hardling, S. M., Marcus, C. L., & Vaughn, B. V. (2012). The AASM Manual for the Scoring of Sleep and Associated Events. *Rules, Terminology and Technical Specifications, Darien, Illinois, American Academy of Sleep Medicine*.

Born, J., & Wilhelm, I. (2012). System consolidation of memory during sleep. *Psychological Research*, *76*(2), 192-203. doi: 10.1007/s00426-011-0335-6

Bradley, M. M., & Lang, P. J. (1994). Measuring emotion: the self-assessment manikin and the semantic differential. *Journal of Behavior Therapy and Experimental Psychiatry*, 25(1), 49-59. doi: 10.1016/0005-7916(94)90063-9

Brenner, C. A., Rumak, S. P., Burns, A. M., & Kieffaber, P. D. (2014). The role of encoding and attention in facial emotional memory: An EEG investigation. *International Journal of Psychophysiology*, *93*(3), 398-410. doi: 10.1016/j.ijpsycho.2014.06.006

Buysse, D. J., Reynolds, C. F., Monk, T. H., Berman, S. R., & Kupfer, D. J. (1989). The Pittsburgh Sleep Quality Index: A new instrument for psychiatric practice and research. *Psychiatry Research*, *28*, 193-213.

Buzsáki, G. (1996). The hippocampo-neocortical dialogue. *Cerebral Cortex*, *6*(2), 81-92.

Cairney, S. A., Durrant, S. J., Hulleman, J., & Lewis, P. A. (2014). Targeted memory reactivation during slow wave sleep facilitates emotional memory consolidation. *Sleep*, *37*(4), 701-707. doi: 10.5665/sleep.3572

Cairney, S. A., Durrant, S. J., Power, R., & Lewis, P. A. (2014). Complementary roles of slow-wave sleep and rapid eye movement sleep in emotional memory consolidation. *Cerebral Cortex*, bht349. doi: 10.1093/cercor/bht349

Canolty, R. T., & Knight, R. T. (2010). The functional role of cross-frequency coupling. *Trends in Cognitive Sciences*, *14*(11), 506-515. doi: 10.1016/j.tics.2010.09.001

Conway, A. R., Kane, M. J., & Engle, R. W. (2003). Working memory capacity and its relation to general intelligence. *Trends in Cognitive Sciences*, *7*(12), 547-552. doi: 10.1016/j.tics.2003.10.005

Corcoran, A. W., Alday, P. M., Schlesewsky, M., & Bornkessel-Schlesewsky, I. (2017). Towards a reliable, automated method of individual alpha frequency (IAF) quantification. bioRxiv, 176792. doi: 10.1101/176792.

Delorme, A., & Makeig, S. (2004). EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. Journal of neuroscience methods, 134(1), 9-21. doi: 10.1016/j.jneumeth.2003.10.009

Diekelmann, S., Wilhelm, I., & Born, J. (2009). The whats and whens of sleep-dependent memory consolidation. *Sleep Medicine Reviews*, *13*(5), 308-321. doi: http://dx.doi.org/10.1016/j.smrv.2008.08.002

Doppelmayr, M., Klimesch, W., Pachinger, T., & Ripper, B. (1998). Individual differences in brain dynamics: important implications for the calculation of event-related band power. *Biological Cybernetics*, *79*(1), 49-57.

Ellenbogen, J. M., Hulbert, J. C., Stickgold, R., Dinges, D. F., & Thompson-Schill, S. L. (2006). Interfering with theories of sleep and memory: Sleep, declarative memory, and associative interference. *Current Biology*, *16*(13), 1290-1294. doi: 10.1016/j.cub.2006.05.024

Everaert, J., & Koster, E. H. (2015). Interactions between emotional attention, encoding, and retrieval of ambiguous information: An eye-tracking study. *Emotion*, *15*(5), 539-543. doi: 10.1037/emo0000063

Faul, F., Erdfelder, E., Lang, A. G., & Buchner, A. (2007). G*Power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behavior Research Methods*, *39*(2), 175-191. doi: 10.3758/BF03193146

Fell, J., & Axmacher, N. (2011). The role of phase synchronization in memory processes. *Nature Reviews Neuroscience*, *12*(2), 105-118. doi: 10.1038/nrn2979

Fox, J. (2003). Effect displays in R for generalised linear models. *Journal of Statistical Software*, *8*(15), 1-27.

Fox, J., & Weisberg, S. (2011). Multivariate linear models in R. *An R Companion to Applied Regression. Los Angeles: Thousand Oaks.*

Genzel, L., Spoormaker, V. I., Konrad, B. N., & Dresler, M. (2015). The role of rapid eye movement sleep for amygdala-related memory processing. *Neurobiology of Learning and Memory*, *122*, 110-121. doi: http://dx.doi.org/10.1016/j.nlm.2015.01.008

Giuditta, A. (2014). Sleep memory processing: the sequential hypothesis. *Frontiers in Systems Neuroscience*, *8*. doi: 10.3389/fnsys.2014.00219

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. *Neurobiology of Learning and Memory*, *99*, 1-9. doi: 10.1016/j.nlm.2012.10.006

Güntekin, B., & Başar, E. (2007). Emotional face expressions are differentiated with brain oscillations. *International Journal of Psychophysiology*, *64*(1), 91–100. doi: 10.1016/j.ijpsycho.2006.07.003

Güntekin, B., & Başar, E. (2014). A review of brain oscillations in perception of faces and emotional pictures. *Neuropsychologia*, *58*, 33-51. doi: 10.1016/j.neuropsychologia.2014.03.014

Hanslmayr, S., Gross, J., Klimesch, W., & Shapiro, K. L. (2011). The role of alpha oscillations in temporal attention. *Brain Research Reviews*, *67*(1), 331-343. doi: 10.1016/j.brainresrev.2011.04.002

Hanslmayr, S., Staudigl, T., & Fellner, M. C. (2012). Oscillatory power decreases and long-term memory: The information via desynchronization hypothesis. *Frontiers in Human Neuroscience*, *6*. doi: 10.3389/fnhum.2012.00074

Heib, D. P., 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? *Journal of Cognitive Neuroscience.* doi: 10.1162/jocn_a_00804

Herbert, C., Junghofer, M., & Kissler, J. (2008). Event-related potentials to emotional adjectives during reading. *Psychophysiology*, *45*(3), 487-498. doi: 10.1111/j.1469-8986.2007.00638.x

Hutchison, I. C., & Rathore, S. (2015). The role of REM theta activity in emotional memory. *Frontiers in Psychology*, *6*, 1439. doi: 10.3389/fpsyg.2015.01439

Jaeger, T. F. (2008). Categorical data analysis: Away from ANOVAs (transformation or not) and towards logit mixed models. *Journal of Memory and Language*, *59*(4), 434-446. doi: 10.1016/j.jml.2007.11.007

Judd, C. M., Westfall, J., & Kenny, D. A. (2012). Treating stimuli as a random factor in social psychology: a new and comprehensive solution to a pervasive but largely ignored problem. *Journal of Personality and Social Psychology*, *103*(1), 54. doi: 10.1037/a0028347

Keenan, E. K., Tiplady, B., Priestley, C. M., & Rogers, P. J. (2014). Naturalistic effects of five days of bedtime caffeine use on sleep, next-day cognitive performance, and mood. *Journal of Caffeine Research*, *4*(1), 13-20. doi:10.1089/jcr.2011.0030

Kensinger, E. A., Garoff-Eaton, R. J., & Schacter, D. L. (2007). Effects of emotion on memory specificity: Memory trade-offs elicited by negative visually arousing stimuli. *Journal of Memory and Language*, *56*(4), 575-591. doi: doi:10.1016/j.jml.2006.05.004

Khader, P. H., Jost, K., Ranganath, C., & Rösler, F. (2010). Theta and alpha oscillations during working-memory maintenance predict successful long-term memory encoding. *Neuroscience Letters*, *468*(3), 339-343. doi: 10.1016/j.neulet.2009.11.028

Klimesch, W. (1997). EEG-alpha rhythms and memory processes. *International Journal of Psychophysiology*, *26*(1), 319-340. doi: 10.1016/S0167-8760(97)00773-3

Klimesch, W. (1999). EEG alpha and theta oscillations reflect cognitive and memory performance: a review and analysis. *Brain Research Reviews*, *29*(2), 169-195. doi: 10.1016/S0165-0173(98)00056-3

Klimesch, W. (2012). Alpha-band oscillations, attention, and controlled access to stored information. *Trends in Cognitive Neuroscience*, *16*(12), 606-617. doi: doi:10.1016/j.tics.2012.10.007

Klimesch, W., Sauseng, P., & Hanslmayr, S. (2007). EEG alpha oscillations: The inhibition–timing hypothesis. *Brain Research Reviews*, *53*(1), 63-88. doi: 10.1016/j.brainresrev.2006.06.003

LaBar, K. S., & Cabeza, R. (2006). Cognitive neuroscience of emotional memory. *Nature Reviews Neuroscience*, *7*(1), 54-64. doi: 10.1038/nrn1825

Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (2008). *International affective picture system (IAPS): Affective ratings of pictures and instruction manual. Technical Report A-8*. University of Florida, Gainesville, FL.

Lang, P., & Bradley, M. M. (2007). The International Affective Picture System (IAPS) in the study of emotion and attention. *Handbook of emotion elicitation and assessment*, *29*.

Lewis, P. A., 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. doi: 10.1016/j.neuropsychologia.2011.05.009

Mackay, D. G., Shafto, M., Taylor, J. K., Marian, D. E., Abrams, L., & Dyer, J. R. (2004). Relations between emotion, memory, and attention: Evidence from taboo Stroop, lexical decision, and immediate memory tasks. *Memory & Cognition*, *32*(3), 474-488. doi: 10.3758/BF03195840

Maddox, G. B., Naveh-Benjamin, M., Old, S., & Kilb, A. (2012). The role of attention in the associative binding of emotionally arousing words. *Psychonomic Bulletin & Review*, *19*(6), 1128-1134. doi: 10.3758/s13423-012-0315-x

Mascetti, L., Foret, A., Schrouff, J., Muto, V., Dideberg, V., Balteau, E., ... & Bours, V. (2013). Concurrent synaptic and systems memory consolidation during sleep. Journal of Neuroscience, 33(24), 10182-10190. doi: 0.1523/JNEUROSCI.0284-13.2013

Mathewson, K. E., Lleras, A., Beck, D. M., Fabiani, M., Ro, T., & Gratton, G. (2011). Pulsed out of awareness: EEG alpha oscillations represent a pulsed-inhibition of ongoing cortical processing. *Frontiers in Psychology*, *2*. doi: 10.3389/fpsyg.2011.00099

Mathôt, S., Schreij, D., & Theeuwes, J. (2012). OpenSesame: An open-source, graphical experiment builder for the social sciences. *Behavior Research Methods*, *44*(2), 314-324. doi:10.3758/s13428-011-0168-7

Mednick, S., Nakayama, K., & Stickgold, R. (2003). Sleep-dependent learning: A nap is as good as a night. *Nature Neuroscience*, *6*(7), 697-698. doi: 10.1038/nn1078

Murty, V. P., Ritchey, M., Adcock, R. A., & LaBar, K. S. (2010). fMRI studies of successful emotional memory encoding: A quantitative meta-analysis. *Neuropsychologia*, *48*(12), 3459-3469. doi: 10.1016/j.neuropsychologia.2010.07.030

Nishida, M., Pearsall, J., Buckner, R. L., & Walker, M. P. (2009). REM sleep, prefrontal theta, and the consolidation of human emotional memory. *Cerebral Cortex*, *19*(5), 1158-1166. doi: 10.1093/cercor/bhn155

Onoda, K., Okamoto, Y., Shishida, K., Hashizume, A., Ueda, K., Yamashita, H., et al. (2007). Anticipation of affective images and event-related desynchronization (ERD) of alpha activity: An MEG study. *Brain Research*, *1151*, 134–141. doi: 10.1016/j.brainres.2007.03.026

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. doi: 10.1037/a0038683

Payne, J. D., Stickgold, R., Swanberg, K., & Kensinger, E. A. (2008). Sleep preferentially enhances memory for emotional components of scenes. *Psychological Science*, *19*(8), 781-788. doi: 10.1111/j.1467-9280.2008.02157.x

Payne, J., Chambers, A. M., & Kensinger, E. A. (2012). Sleep promotes lasting changes in selective memory for emotional scenes. *Frontier in Integrative Neuroscience, 6*. doi: 10.3389/fnint.2012.00108

Payne, L., & Sekuler, R. (2014). The importance of ignoring: Alpha oscillations protect selectivity. *Current Directions in Psychological Science*, *23*(3), 171-177. doi: 10.1177/0963721414529145

Peterson, E. J., & Voytek, B. (2017). Alpha oscillations control cortical gain by modulating excitatory-inhibitory background activity. *bioRxiv*, 185074. doi: 10.1101/185074.

Pfurtscheller, G., Stancak, A., & Neuper, C. (1996). Event-related synchronization (ERS) in the alpha band—an electrophysiological correlate of cortical idling: a review. *International Journal of Psychophysiology*, *24*(1), 39-46. doi: 10.1016/S0167-8760(96)00066-9

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. doi: 10.1371/journal.pone.0065098

Rasch, B., & Born, J. (2013). About sleep's role in memory. *Physiological Review*, *93*(2), 681-786. doi: 10.1152/physrev.00032.2012

Rasch, B., & Born, J. (2015). In search of a role of REM sleep in memory formation. *Neurobiology of Learning and Memory, 122*, 1-3. doi: 10.1016/j.nlm.2015.04.012

Riggs, L., McQuiggan, D. A., Farb, N., Anderson, A. K., & Ryan, J. D. (2011). The role of overt attention in emotion-modulated memory. *Emotion*, *11*(4), 776. doi: 10.1037/a0022591

Sadaghiani, S., & Kleinschmidt, A. (2016). Brain networks and α-oscillations: structural and functional foundations of cognitive control. *Trends in Cognitive Sciences, 20*(11), 805-817. doi: 10.1016/j.tics.2016.09.004

Sakaki, M., Niki, K., & Mather, M. (2012). Beyond arousal and valence: The importance of the biological versus social relevance of emotional stimuli. *Cognitive, Affective, & Behavioral Neuroscience*, *12*(1), 115-139. doi: 10.3758/s13415-011-0062-x

Saletin, J. M., & Walker, M. P. (2012). Nocturnal mnemonics: Sleep and hippocampal memory processing. *Frontiers in Neurology*, *3*, 59. doi: http://dx.doi.org/10.3389/fneur.2012.00059

Scheffzük, C., Kukushka, V. I., Vyssotski, A. L., Draguhn, A., Tort, A. B., & Brankačk, J. (2011). Selective coupling between theta phase and neocortical fast gamma oscillations during REM-sleep in mice. *PLoS One*, *6*(12), e28489-e28489.

Schreiner, T., & Rasch, B. (2014). Boosting vocabulary learning by verbal cueing during sleep. *Cerebral Cortex, 25*(11), 4169-4179. doi: 10.1093/cercor/bhu139

Schupp, H. T., Flaisch, T., Stockburger, J., & Junghofer, M. (2006). Emotion and attention: Event-related brain potential studies. *Progress in Brain Research*, *156*, 31-51. doi: 10.1016/S0079-6123(06)56002-9

Schwarz, G. (1978). Estimating the dimension of a model. *The Annals of Statistics, 6*(2), 461-464.

Shalev, L., Ben-Simon, A., Mevorach, C., Cohen, Y., & Tsal, Y. (2011). Conjunctive Continuous Performance Task (CCPT) — A pure measure of sustained attention. *Neuropsychologia*, *49*(9), 2584-2591. doi: 10.1016/j.neuropsychologia.2011.05.006

Smith, A. P., Henson, R. N., Dolan, R. J., & Rugg, M. D. (2004). fMRI correlates of the episodic retrieval of emotional contexts. *NeuroImage*, *22*(2), 868-878. doi: 10.1016/j.neuroimage.2004.01.049

Stickgold, R., & Walker, M. P. (2013). Sleep-dependent memory triage: Evolving generalization through selective processing. *Nature Neuroscience, 16*(2), 139-145. doi: 10.1038/nn.3303

Talmi, D. (2013). Enhanced emotional memory: Cognitive and neural mechanisms. *Current Directions in Psychological Science, 22*(6), 430-436. doi: 10.1177/0963721413498893

Tassi, P., & Muzet, A. (2000). Sleep inertia. *Sleep Medicine Reviews*, *4*(4), 341-353. doi: 10.1053/smrv.2000.0098

Tononi, G., & Cirelli, C. (2012). Time to be SHY? Some comments on sleep and synaptic homeostasis. *Neural Plasticity*, 2012. doi: 10.1155/2012/415250

Tononi, G., & Cirelli, C. (2014). Sleep and the price of plasticity: from synaptic and cellular homeostasis to memory consolidation and integration. *Neuron, 81*(1), 12-34. doi: 10.1016/j.neuron.2013.12.025

Uribe, C. E., Garcia, A., & Tomaz C. (2011). Electroencephalographic brain dynamics of memory encoding in emotionally arousing context. *Frontiers in Behavioural Neuroscience*, *5*(35), 1-9. doi: 10.3389/fnbeh.2011.00035

Uusberg, A., Uibo, H., Kreegipuu, K., & Allik, J. (2013). EEG alpha and cortical inhibition in affective attention. *International Journal of Psychophysiology*, *89*(1), 26-36. doi: 10.1016/j.ijpsycho.2013.04.020

Van Dongen, H. P., Olofsen, E., Dinges, D. F., & Maislin, G. (2004). Mixed-model regression analysis and dealing with interindividual differences. *Methods in enzymology*, *384*, 139-171.

Vertes, R. P. (2005). Hippocampal theta rhythm: A tag for short-term memory. *Hippocampus, 15*(7), 923-935.

Vuilleumier, P. (2005). How brains beware: Neural mechanisms of emotional attention. *Trends in Cognitive Sciences*, *9*(12), 585-594. doi: 10.1016/j.tics.2005.10.011

Wagner, U., Gais, S., & Born, J. (2001). Emotional memory formation is enhanced across sleep intervals with high amounts of rapid eye movement sleep. *Learning & Memory*, *8*(2), 112-119. doi: 10.1101/lm.36801

Walz, J. M., Goldman, R. I., Carapezza, M., Muraskin, J., Brown, T. R., & Sajda, P. (2015). Prestimulus EEG alpha oscillations modulate task-related fMRI BOLD responses to auditory stimuli. *Neuroimage*, *113*(1), 153-163. doi: doi:10.1016/j.neuroimage.2015.03.028

Wang, L., & Bastiaansen, M. (2014). Oscillatory brain dynamics associated with the automatic processing of emotion in words. *Brain & Language*, *137*, 120-129. doi: 10.1016/j.bandl.2014.07.011

Wechsler, D. (2011). *Wechsler Abbreviated Scale of Intelligence–Second Edition Manual*. Bloomington, MN: Pearson.

Welch, P. (1967). The use of fast fourier transform for the estimation of power spectra: a method based on time averaging over short, modified periodograms. *IEEE Transactions on Audio and Electroacoustics*, 70-73.

Wickham, H. (2009). ggplot2: Elegant Graphics for Data Analysis Springer-Verlag. *New York*.

Yordanova, J., Kolev, V., & Polich, J. (2001). P300 and alpha event-related desynchronization (ERD). *Psychophysiology*, *38*(1), 143-152. doi: 10.1111/1469-8986.3810143