

Sleep spindles provide indirect support to the consolidation of emotional encoding contexts

- Scott A. Cairney^{a,c,*,}
- Simon J. Durrant^{b,}
- Rebecca Jackson^{c,}
- Penelope A. Lewis^{c,}
- ^a Department of Psychology, University of York, Heslington, York YO10 5DD, UK
- ^b School of Psychology, University of Lincoln, Brayford Pool, Lincoln LN6 7TS, UK
- ^c School of Psychological Sciences, University of Manchester, Oxford Road, Manchester M13 9PL, UK

Received 30 July 2014, Revised 4 September 2014, Accepted 7 September 2014, Available online 16 September 2014

Open Access funded by Engineering and Physical Sciences Research Council

Under a Creative Commons license
doi:10.1016/j.neuropsychologia.2014.09.016

Highlights

•

The aspects of sleep that influence emotional memory contexts were examined.

•

Emotional and neutral contexts were better remembered after sleep than wake.

•

Sleep spindles predicted increased forgetting of neutral contexts.

•

Sleep spindles also predicted slowed response times for neutral contexts.

•

Spindles support emotional contexts indirectly by suppressing neutral contexts.

Abstract

Emotional memories tend to be strengthened ahead of neutral memories during sleep-dependent consolidation. In recent work, however, we found that this is not the case when emotion pertains to the contextual features of a memory instead of its central constructs, suggesting that emotional contexts are influenced by distinct properties of sleep. We therefore

examined the sleep-specific mechanisms supporting representations of emotional context and asked whether these differ to those already implicated in central emotional memory processing, such as rapid eye movement sleep (REM). Participants encoded neutral foreground images that were each associated with an emotionally negative or neutral background (context) image. Immediate and delayed tests for the emotionality of the foreground/background image association were separated by a 4-h consolidation period, which consisted of either total wakefulness or included a 2-h polysomnographically monitored nap. Although memory for negative contexts was not associated with REM, or any other parameter of sleep, sleep spindles (12–15 Hz) predicted increased forgetting and slowed response times for neutral contexts. Together with prior work linking spindles to emotional memory processing, our data may suggest that spindles provide multi-layered support to emotionally salient memories in sleep, with the nature of such effects depending on whether the emotionality of these memories pertains to their central or contextual features. Therefore, whereas spindles may mediate a direct strengthening of central emotional information, as suggested in prior work, they may also provide concurrent indirect support to emotional contexts by working to suppress non-salient neutral contexts.

Keywords

- Emotion;
- Context;
- Memory;
- Consolidation;
- Sleep spindles

1. Introduction

Evidence obtained from both behavioural and physiological investigations indicates that memory consolidation is enhanced across overnight sleep relative to corresponding periods of daytime wakefulness (Born et al., 2006, Diekelmann, 2014, Diekelmann and Born, 2010, Ellenbogen et al., 2006, Paller and Voss, 2004, Rasch and Born, 2013, Stickgold, 2005 and Walker, 2008). Such sleep-dependent consolidation has been reported across a variety of declarative learning materials including word pairs (Gais et al., 2006 and Plihal and Born, 1997), category exemplars (Cairney, Durrant, Musgrove, & Lewis, 2011) and object-location associations (Rasch et al., 2007 and Wilhelm et al., 2008), and has also been shown across daytime naps (Lau et al., 2010, Tucker et al., 2006 and Wamsley et al., 2010).

Rather than impacting upon the consolidation of all newly-learned memories equally, recent work has suggested that sleep-dependent memory processes operate in a more discerning manner, such that information is selectively consolidated on the basis of its salience or relevance for future recall (Born and Wilhelm, 2012, Payne and Kensinger, 2010, Rasch and Born, 2013, Stickgold, 2013 and Stickgold and Walker, 2013). Accordingly,

emotionally negative memories are often strengthened over sleep to a greater extent than their neutral counterparts (Holland and Lewis, 2007 and Hu et al., 2006), with several studies linking such effects to rapid eye movement sleep (REM) (Groch et al., 2013, Hockley, 2008, Nishida et al., 2009 and Wagner et al., 2001), although see also Baran, Pace-Schott, Ericson, and Spencer (2012). In a seminal study by Payne, Stickgold, Swanberg, and Kensinger (2008), participants encoded various photographic scenes before a night of sleep or a day of wakefulness. Importantly, each scene contained a neutral background image and a superimposed object image, which was either emotionally negative (emotional scene) or neutral (neutral scene). Whereas time spent awake led to forgetting of the entire emotional scene, a night of sleep preserved representations of the negative objects, but not the neutral objects or the neutral backgrounds associated with either object type, suggesting that sleep-specific processes targeted only the centrally affective components of these newly-formed emotional memories.

In prior work, however, we showed that this effect does not hold true when the emotionality of a novel representation pertains to its contextual features, rather than the central memory information (Lewis, Cairney, Manning, & Critchley, 2011). In this study, participants encoded several neutral object images that were each superimposed on a negative or neutral background (context) image. After a period of sleep or equivalent wakefulness, participants were presented with each object image alone and asked to recall the emotionality of its associated background context. Contextual associations were generally better remembered after sleep than wake, but there was no selective sleep-related improvement in the recall of negative contexts. One potential reason for this finding is that centrally emotional memories are influenced by sleep in different manners to representations of emotional context. Accordingly, whereas Payne, Chambers, and Kensinger (2012) linked negative object retention to REM in recent work, distinct properties of sleep may support affective contextual information. Sleep spindles, for example, which are electroencephalographic (EEG) oscillations in the ~12–15 Hz frequency range, have been linked to the consolidation of both contextual (van der Helm, Gujar, Nishida, & Walker, 2011) and emotional representations (Kaestner, Wixted, & Mednick, 2013), and are thought to be integral to selective memory processing during sleep (Born and Wilhelm, 2012 and Stickgold and Walker, 2013). In one study, spindles predicted better recall for newly-learned memories when they were made more salient prior to sleep (Wilhelm et al., 2011), whereas another study linked spindles to the retention of items that individuals were instructed to remember, as compared to items that they were instructed to forget (Saletin, Goldstein, & Walker, 2011). It is therefore possible, that spindles support emotionally salient information that is embedded within the context of newly-acquired memory representations.

In the current article, we provide the first report on an analysis of polysomnography (PSG) data recorded from individuals who napped between immediate and delayed testing for emotionally negative and neutral context memories. This allowed us to examine the sleep-specific mechanisms underpinning emotional memory consolidation in the contextual domain, and ask whether such mechanisms differ to those that support

central emotional memory processing. Following the suggestion that sleep spindles may benefit emotionally salient contextual information, we predicted that these oscillations would support associations of negative context.

2. Material and methods

2.1. Participants

Thirty-eight (10 male) healthy participants (mean age 20.92, [S.D.±3.70]) free from any history of sleep, psychiatric or neurological disorders (as evaluated with pre-study screening questionnaires and telephone interviews) were recruited on a voluntary basis for two experimental sessions. Participants gave written informed consent in line with the School of Psychological Sciences Research Ethics Committee, University of Manchester, and refrained from consuming alcoholic or caffeinated products for 24 h prior to the study and throughout the study period. Participants were assigned to one of two experimental groups: 'nap' or 'wake', both contained 19 participants (5 male) with equivalent ages (wake group mean: 21.32 [S.D.±3.65], nap group mean: 20.53 [S.D.±3.78], $t(36)=0.66$; $p=0.52$). In order to check for group differences in alertness, participants completed the Stanford Sleepiness Scale (Hoddes, Zarcone, Smythe, Phillips, & Dement, 1973) in both experimental sessions. As an explicit test of alertness related to homeostatic sleep pressure, we also calculated correlation coefficients between the amount of SWS (min) obtained by participants in the nap group and all post-sleep retrieval response times (RTs) (Cairney et al., in press, Durrant et al., 2013 and Durrant et al., 2011).

2.2. Experimental task

To investigate the relationship between sleep and emotional context memory, we employed an established source memory paradigm (Lewis et al., 2011, Smith et al., 2005 and Smith et al., 2006). At encoding, neutral foreground (object) images were superimposed on emotionally negative or neutral background (context) images. In the subsequent retrieval phases, participants were presented with object images alone and, for each, asked to indicate if it was old or new, and (if old) whether the context image it had been associated with at encoding was emotionally negative or neutral. Task procedures are illustrated in Fig. 1A.

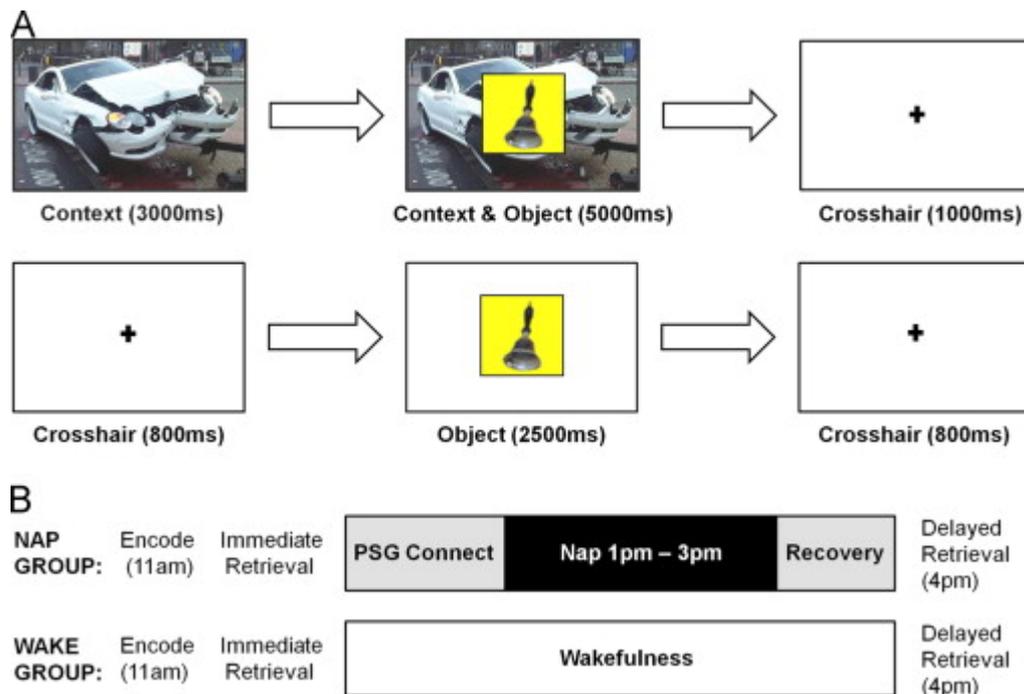


Fig. 1.

(A) Encoding and retrieval tasks and (B) study procedures. (A) At encoding, participants were presented with a context image and asked to rate its emotional valence (1=highly negative, 5=neutral, and 9=highly positive). Shortly afterwards, an object image was placed on top of the context image and participants were asked to make an association between them. At retrieval, participants saw the object image alone and were asked to make one of four responses: 1) 'the image is new', 2) 'the image is old and was originally paired with a negative context image', 3) 'the image is old and was originally paired with a neutral context image' and 4) 'the image is old but I can't remember if the context image was neutral or negative'. (B) Study procedures for the nap group and wake group.

2.3. Stimuli

One hundred and thirty-one images were taken from the International Affective Picture System (IAPS) (Lang, Bradley, & Cuthbert, 2005) and supplemented with 29 images from the internet to create two sets of 80 negative and 80 neutral context images, which were counterbalanced for content (people/no people). IAPS pictures range from everyday scenes to images of injury, violence, decay and contaminated foods, and are rated on 9-point scales for both emotional valence (1=extremely negative, 5=neutral, and 9=extremely positive) and emotional arousal (1=very low arousal/boring and 9=very high arousal/exciting). The negative and neutral context image sets were significantly different in terms of mean valence rating (negative: 2.38 [S.D.±0.67], neutral: 5.14 [S.D.±0.46], $t(63)=23.28$; $p<0.0001$) and mean arousal rating (negative: 5.81 [S.D.±0.84], neutral: 3.36 [S.D.±0.76], $t(63)=17.25$; $p<0.0001$). Three hundred and twenty neutral object images were taken from the Hemera objects collection: <http://desktoppub.about.com/cs/stockphotovendors/gr/photoobjects1-2.htm> and each appeared on a square yellow background. Avoiding instances where a semantic relationship between an object and context image could be easily established, eight unique sets of 160 context/object image pairs were pseudorandomly generated for encoding. Lists 1–4 used one half of the 320 object images (160), whereas lists 5–8 used the

remaining half. The use of these lists was counterbalanced across participants.

2.4. Equipment

2.4.1. Task

The experimental tasks were created using Cogent 2000 (Functional Imaging Laboratory, University College London) and were both written and implemented using MatLab® (version 6.5) on a desktop PC with a dual-core Xeon processor and a 20" computer screen. At encoding, participant responses were recorded using the PC keyboard, whereas retrieval session responses were recorded with a serial multi-button box attached to a Domino 2 microcontroller from Micromint®, which had a time resolution of approximately 1 ms.

2.4.2. PSG

Sleep monitoring was carried out using an Embla® N7000 PSG system with RemLogic® (version 1.1) software. Silver–silver chloride (Ag–AgCl) electrodes were attached using EC2® electrogel after the scalp was cleaned with NuPrep® exfoliating agent. EEG scalp electrodes were attached according to the international 10–20 system at six standardised locations: central (C3 and C4), frontal (F3 and F4) and occipital (O1 and O2), and each was referenced to the contralateral mastoid (A1 or A2). Electrooculography electrodes were attached next to the left and right eye, and electromyography electrodes were attached to the mentalis and bilateral submentalis. All electrodes were verified to have a connection impedance of less than 5 k Ω . All signals were digitally sampled at a rate of 200 Hz.

2.5. Procedure

2.5.1. Encoding (11 am)

Study procedures are illustrated in Fig. 1B. For each encoding trial, a negative or neutral context image was displayed for 3000 ms before a neutral object image was superimposed for a further 5000 ms. Both images were then replaced with a fixation cross for 1000 ms. When the context image appeared, participants were asked to rate its emotional valence on a scale of 1–9 (1=highly negative and 9=highly positive) using the corresponding keys on the keyboard. Participants were then required to form a mental association between the context image and the subsequently appearing object image, pressing the space bar to indicate that such an association had been formed. To facilitate learning, the 160 context/object image pairs were separated into two randomised blocks of 80 trials (40 negative and 40 neutral).

2.5.2. Immediate retrieval test

Immediately after each encoding block, participants' context memory was tested. In both retrieval tests, the 80 learned objects and 20 new objects (taken from the 160 images not used at encoding) were presented in random order, each for 2500 ms with an 800 ms inter-stimulus fixation

cross. Importantly, object images were presented alone without the associated context image. For each object image, participants were instructed to make one of four possible responses as quickly and accurately as possible: 1) 'the image is new', 2) 'the image is old and was originally paired with a negative background image', 3) 'the image is old and was originally paired with a neutral background image' and 4) 'the image is old but I can't remember if the background image was neutral or negative'. Participants took a short break (<1 min) after completing the immediate test for the first encoding block and then commenced the second encoding block followed by the other immediate test, which included another 20 novel images. Data from the two immediate tests were combined and provided an index of pre-consolidation performance.

2.5.3. Retention interval (12 pm)

After the immediate tests, participants were assigned to a 4 h retention interval of wakefulness (wake group), or an equivalent period that also contained a 2 h nap (nap group). Participants in the wake group were free to leave the study area during this time, but were asked not to sleep, exercise or engage in any form of active learning. Participants in the nap group, however, were first connected to a PSG unit (12 pm-1 pm) and then asked to sleep in a bedroom within the sleep research laboratory of the University of Manchester for approximately 2 h (1–3 pm). After waking, participants were disconnected from the PSG unit and given an opportunity to wash their hair (3–3.30 pm), before taking a further 30 min break to ensure recovery from sleep inertia (3.30–4 pm).

2.5.4. Delayed test (4 pm)

Participants then completed a delayed test session. This followed the same procedures as the immediate tests described above, except that the 40 new images used in the first and second testing blocks were replaced. Accordingly, participants saw a total of 80 new object images: 40 at immediate testing and 40 at delayed testing. Data from the two delayed tests were combined and provided an index of post-consolidation performance.

2.6. Data analysis

2.6.1. Behavioural data

We assessed the consolidation of context memory with an index of forgetting (immediate retrieval score – delayed retrieval score; adapted from Lewis et al., 2011) and an index of RT change (delayed RT – immediate RT) for correctly recalled contexts. A 2×2 mixed ANOVA design was used with the between subjects factor 'Group' (wake/nap) and the within subjects factor 'Emotion' (negative/neutral). All behavioural data were analysed with SPSS statistical software (version 16.0) with a two-tailed $p < 0.05$ considered significant.

2.6.2. Sleep scoring

PSG sleep recordings were independently scored by two experienced sleep researchers (SAC & SJD) using RemLogic© (version 1.1) software. Sleep data were categorised into 30 s epochs and scored on the referenced central electrodes (C3-A2 and C4-A1) according to the standardised sleep scoring criteria of Rechtschaffen and Kales (1968), with sleep stages three and four collectively scored as SWS. After scoring, sleep data were partitioned in terms of the duration of time (min) spent in each sleep stage: stage one sleep (S1), stage two sleep (S2), SWS and REM. Significant correlations between sleep stages and measures of behaviour (forgetting and RT change) underwent a traditional Bonferroni correction for multiple comparisons (α (0.05)/number of tests (8)<0.006).

2.6.3. Sleep spindles

Epochs scored as S2 or SWS were extracted from each EEG channel and, following artefact rejection, bandpass filtered at 12–15 Hz (all spindles), 12–13.5 Hz (slow spindles) and 13.5–15 Hz (fast spindles) using a linear finite impulse response filter in EEGLAB (version 10.0). An automated spindle detection algorithm (Ferrarelli et al., 2007) counted discrete spindle events in each EEG channel as amplitude fluctuations within the filtered time series which exceeded a pre-determined threshold of eight times the mean channel amplitude. Accordingly, sleep spindles were counted at central (C3-A2, C4-A1), frontal (F3-A2, F4-A1) and occipital (O1-A2, O2-A1) EEG channels for each participant, though noisy channels were removed from our analyses. This spindle detection algorithm has been used in several previous studies (Cairney et al., 2014, Nishida and Walker, 2007 and Tamminen et al., 2010). Significant correlations between spindles and measures of behaviour (forgetting and RT change) underwent a traditional Bonferroni correction for multiple comparisons (α (0.05)/number of tests (12)<0.004).

3. Results

3.1. Pre-study sleep data

Sleep questionnaires revealed that there was no significant difference between the wake and nap groups in terms of the mean hours slept during the night preceding the study (wake group: 7.89 [S.D.±1.06], nap group: 7.45 [S.D.±1.05], $t(36)=1.30$; $p=0.20$) or mean hours slept in a typical night (wake group: 7.74 [S.D.±0.93], nap group: 7.53 [S.D.±0.70], $t(36)=0.79$; $p=0.44$).

3.2. Alertness

Mean alertness scores, obtained using the Stanford Sleepiness Scale, were equivalent for the nap and wake groups at both immediate testing (wake group: 2.63 [S.D.±0.76], nap group: 2.53 [S.D.±0.61], $t(36)=0.47$; $p=0.64$) and delayed testing (wake group: 2.79 [S.D.±1.13], nap group: 2.53 [S.D.±0.77], $t(36)=0.84$; $p=0.41$). Neither the wake group nor the nap group showed significant differences in mean alertness scores between the immediate and delayed tests (wake group: $t(18)=0.59$; $p=0.56$, nap group: $t(18)=0.00$; $p=1.00$). In an additional test of alertness related to

homeostatic sleep pressure, no significant relationship was found between the amount of SWS (mins) obtained by nap group participants and all RTs for either neutral ($r=0.15$; $p=0.53$) or negative ($r=0.12$; $p=0.64$) contexts at delayed testing.

3.3. Behaviour

The impact of retention interval upon the consolidation of context memory was quantified with a measure of forgetting and RT change for correctly recalled contexts. A 2x2 mixed ANOVA with the between subjects factor 'Group' (wake/nap) and the within subjects factor 'Emotion' (negative/neutral) showed that participants who napped during the retention interval forgot fewer contexts ($F(1,36)=5.51$; $p=0.024$, for details see Lewis et al. (2011)) and exhibited more RT speeding for correctly recalled contexts ($F(1,36)=4.35$; $p=0.044$) than those who remained awake. There was no main effect of Emotion in either forgetting ($F(1,36)=0.09$; $p=0.77$) or RT change ($F(1,36)=0.43$; $p=0.52$), and neither measure revealed an interaction between factors (forgetting: $F(1,36)=0.02$; $p=0.90$, RT change: $F(1,36)=0.17$; $p=0.68$).

3.4. PSG

3.4.1. Sleep spindles

Sleep spindle data is available in Table 1. Spindles counted at the right frontal EEG channel (F4-A1) predicted the extent to which neutral contexts were forgotten over sleep ($r=0.63$; $p=0.004$), but showed no such relationship with negative context forgetting ($r=-0.14$; $p=0.58$) (see Fig. 2A). A Hotelling's t -test also revealed that these correlations were significantly different ($t(16)=2.79$; $p=0.013$). To directly examine whether sleep spindles were more strongly associated with neutral over emotional context forgetting, we created an emotional context score (ECS) for each participant in the nap group [ECS=neutral context forgetting–emotional context forgetting]. A positive ECS showed that fewer emotional (relative to neutral) contexts were forgotten, whereas a negative ECS showed that fewer neutral (relative to emotional) contexts were forgotten. Importantly, F4-A1 spindles predicted a strongly positive ECS ($r=0.62$; $p=0.004$), further suggesting that spindles occurring at right frontal cortex support the decay of neutral contextual associations. No significant relationship was found between spindles counted at other EEG channels and either neutral context forgetting (F3-A2: $r=0.45$; $p=0.07$, C3-A2: $r=0.28$; $p=0.25$, C4-A1: $r=0.40$; $p=0.09$, O1-A2: $r=0.12$; $p=0.70$, O2-A1: $r=0.10$; $p=0.74$) or negative context forgetting (F3-A2: $r=-0.21$; $p=0.41$, C3-A2: $r=-0.11$; $p=0.67$, C4-A1: $r=-0.13$; $p=0.59$, O1-A2: $r=0.42$; $p=0.15$, O2-A1: $r=-0.26$; $p=0.38$).

Table 1.

Sleep spindle count per EEG channel (nap group mean).

C3	C4	F3	F4	O1	O2
56.06 (S.D.±29.34)	52.42 (S.D.±30.15)	102.41 (S.D.±55.80)	93.53 (S.D.±59.29)	17.38 (S.D.±12.76)	15.92 (S.D.±10.64)

Table options

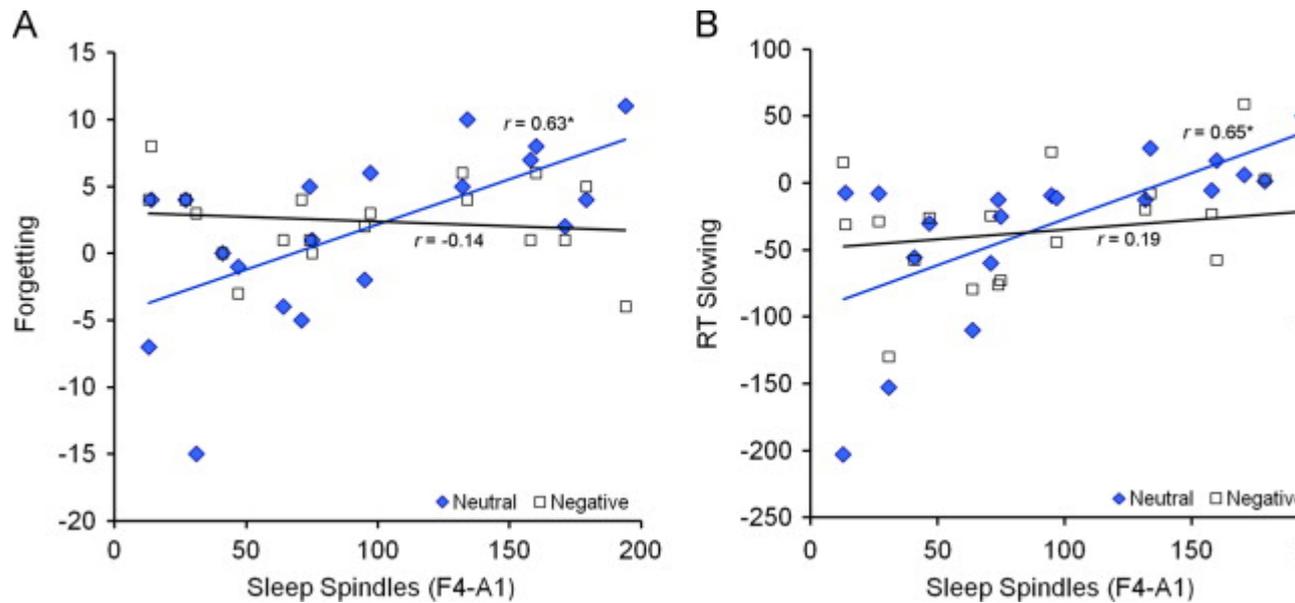


Fig. 2.

Spindle analysis. (A) Sleep spindles (F4-A1) predicted increased forgetting of neutral contexts. (B) Sleep spindles (F4-A1) predicted slowed response times (RTs) for correctly retrieved neutral contexts. Statistically significant correlations are denoted with a '*'.[†]

F4-A1 spindles also predicted slower RTs for correctly recalled neutral contexts across sleep ($r=0.65$; $p=0.002$), with no such relationship observed for negative contexts ($r=0.19$; $p=0.45$) (see Fig. 2B), although a Hotelling's t -test revealed that the difference between these correlations was not statistically significant ($t(16)=1.91$; $p=0.07$). While spindles counted at the right central EEG channel (C4-A1) also predicted a slowing of RTs for neutral contexts ($r=0.52$; $p=0.024$), this correlation did not survive correction for multiple comparisons. Spindles counted at other EEG channels did not significantly correlate with a change in RTs for either neutral contexts (F3-A2: $r=0.45$; $p=0.07$, C3-A2: $r=0.40$; $p=0.10$, O1-A2: $r=-0.13$; $p=0.66$, O2-A1: $r=-0.01$; $p=0.97$) or negative contexts (F3-A2: $r=0.14$; $p=0.59$, C3-A2: $r=0.14$; $p=0.58$, C4-A1: $r=0.09$; $p=0.71$, O1-A2: $r=-0.10$; $p=0.74$, O2-A1: $r<0.0001$; $p=1.00$).

To investigate these spindle-specific relationships further, we conducted a separate examination of slow (12–13.5 Hz) and fast (13.5–15 Hz) frequency spindles counted at the F4-A1 channel. Both spindle subtypes predicted neutral context forgetting, although the correlation with slow spindles was marginally below the multiple comparisons correction threshold (slow spindles: $r=0.62$; $p=0.005$, fast spindles: $r=0.62$; $p=0.004$). Neither spindle subtype predicted negative context forgetting (slow spindles: $r=-0.19$; $p=0.43$, fast spindles: $r=-0.09$; $p=0.70$), and Hotelling's t -tests revealed that the correlations between each spindle subtype and neutral context forgetting were significantly different to those with negative context forgetting (slow spindles: $t(16)=2.97$; $p=0.009$, fast spindles: $t(16)=2.59$; $p=0.02$). Slow and fast F4-A1 spindles also predicted a strongly positive ECS (slow spindles: $r=0.64$; $p=0.003$, fast spindles: $r=0.60$; $p=0.007$).

A slowing of RTs for neutral contexts was also predicted by both fast and slow F4-A1 spindles, but, again, the correlation with slow spindles was marginally below the multiple comparisons correction threshold (slow

spindles: $r=0.61$; $p=0.006$, fast spindles: $r=0.67$; $p=0.002$). Neither spindle subtype predicted RT changes for negative contexts (slow spindles: $r=0.08$; $p=0.74$, fast spindles: $r=0.28$; $p=0.25$), but Hotelling's t -tests showed that the correlations between each spindle subtype and RT slowing for neutral contexts were not significantly different to those with RT changes for negative contexts (slow spindles: $t(16)=2.03$; $p=0.06$, fast spindles: $t(16)=1.66$; $p=0.12$).

3.4.2. Stages of sleep

Sleep stage data is available in Table 2. Time spent in S2 predicted both reduced forgetting of negative contexts ($r=-0.46$; $p=0.049$), and RT speeding for correctly recalled negative contexts ($r=-0.55$; $p=0.016$), although neither correlation survived correction for multiple comparisons. While no relationship was found between negative context forgetting and any other stage of sleep (S1: $r=-0.14$; $p=0.56$, SWS: $r=0.22$; $p=0.37$, REM: $r=-0.12$; $p=0.64$), time spent in SWS predicted a slowing of RTs for negative contexts ($r=0.52$; $p=0.023$), although, again, this correlation did not survive multiple comparisons correction. No relationship was found between changes in negative context RT and time spent in S1 ($r=0.17$; $p=0.48$) or REM ($r=0.07$; $p=0.78$).

Table 2.

Minutes in each sleep stage and total sleep time (nap group mean).

Stage 1	Stage 2	SWS	REM	TST
15 (S.D. \pm 8.11)	50.50 (S.D. \pm 17.12)	18.87 (S.D. \pm 11.42)	22.13 (S.D. \pm 14.51)	106.50 (S.D. \pm 28.45)

SWS=Slow-wave sleep, REM=Rapid eye movement sleep, TST=Total sleep time.

For neutral contexts, no stage of sleep significantly predicted either forgetting (S1: $r=-0.07$; $p=0.76$, S2: $r=0.07$; $p=0.78$, SWS: $r=0.26$; $p=0.27$, REM: $r=-0.11$) or changes in RT (S1: $r=-0.24$; $p=0.33$, S2: $r=0.14$; $p=0.58$, SWS: $r=0.44$; $p=0.06$, REM: $r=0.08$; $p=0.74$).

4. Discussion

Research has indicated that central components of emotional memory are preferentially consolidated over sleep, with the extent of such enhancements depending on time spent in REM (Payne et al., 2012, Payne and Kensinger, 2011 and Payne et al., 2008). In prior work (Lewis et al., 2011), however, we demonstrated that the selective benefits of sleep for emotional memory do not emerge when the emotionality of a novel representation relates instead to its contextual features, thereby suggesting that emotional contexts are influenced by different properties of sleep to those that support central emotional memory information. Here, through careful analysis of previously unreported PSG data, we investigated the sleep-specific mechanisms that support affective contextual representations. Intriguingly, sleep spindles occurring at right frontal cortex predicted both increased forgetting and slowed RTs for neutral contexts, but not negative contexts. In view of these findings, it is possible that frontally occurring spindles work to suppress neutral contexts, and in doing so provide indirect support to the consolidation of emotionally salient contextual information.

4.1. Sleep spindles and emotional contexts

Sleep spindles, which originate in the thalamus and propagate to widespread cortical regions (De Gennaro & Ferrara, 2003), are robustly associated with offline memory processes (Astori et al., 2013, Diekelmann, 2014 and Rasch and Born, 2013). Human studies have reported increased spindle activity after learning (Gais et al., 2002 and Schmidt et al., 2006), as well as predictive relationships between spindle activity and subsequent memory performance; an effect observed across naturally occurring sleep (Clemens et al., 2005 and Schabus et al., 2004) and following pharmacological manipulations of spindle density (Mednick et al., 2013). Because memory systems are constrained by limited processing resources, the ability to prioritise relevant memories for consolidation and future recall is critical to survival. It has been suggested that such discriminatory memory processing is enhanced during sleep (Stickgold, 2013 and Stickgold and Walker, 2013), with sleep spindles, amongst other factors, playing a central role in this selective memory retention (Born and Wilhelm, 2012 and Rasch and Born, 2013). Accordingly, spindle activity has been found to increase when newly-learned memories are made more salient prior to sleep, with such increases also predicting subsequent memory performance (Wilhelm et al., 2011). Moreover, a recent study found that pharmacological increases in spindle density predicted better retention of emotionally salient memories; specifically those that were negatively valenced or highly arousing (Kaestner et al., 2013). In our current data, spindles showed no relationship with memory for negative contexts, but were instead associated with forgetting and RT slowing for neutral contexts. A speculative possibility, therefore, is that spindles provide multi-layered support to discriminatory memory processing, with the nature of this support depending on both the level of salience attributed to a newly-formed representation and whether that salience pertains to its focal or contextual features. Hence, whereas spindles may fortify centrally salient emotional memories directly, they may also provide concurrent indirect support to contextually affective representations by suppressing non-salient neutral contexts that were encoded at the same time. In such a case, the impacts of sleep spindles for emotional memory consolidation may also interact with those related to other parameters of sleep. During REM, for example, levels of the neurotransmitter acetylcholine, which appears to co-regulate the effects of emotion on consolidation (Introini-Collison et al., 1996 and Power and McGaugh, 2002), are twice as high as those observed in wakefulness (Marrosu et al., 1995), and this sleep stage has been linked to emotional memory retention in a number of prior reports (Groch et al., 2013, Nishida et al., 2009 and Wagner et al., 2001), although see also Baran et al. (2012). The sleep spindles of non-REM and increased cholinergic activity of REM may therefore both contribute to emotional plasticity over sleep. Notably, in addition to strengthening newly-acquired emotional memories, REM is thought to support a depotentiation of the affective tone associated with such memories at encoding (Walker, 2009 and Walker and van der Helm, 2009), and recent studies have suggested that affective contextual unbinding requires several nights of sleep to complete (Deliens et al., 2013, Deliens et al., 2013 and Deliens and Peigneux, 2013). Accordingly, an inhibitory influence of sleep spindles upon neutral contexts may reflect a

preliminary stage of sleep-dependent consolidation, which complements the latter memory effects of REM to support a broader decontextualisation of new information, although this is a speculative possibility for future research. While our data showed that forgetting and RT slowing for neutral contexts were predicted by both slow (12–13.5 Hz) and fast (13.5–15 Hz) spindle subtypes, the relationships between slow spindles and behavioural change fell beneath the threshold for multiple comparisons. It is possible, therefore, that fast spindles hold a particularly prominent role in suppressing non-salient context memories. Indeed, fast spindles are associated with greater hippocampal activity than slow spindles (Dang-Vu et al., 2010 and Schabus et al., 2007), suggesting that these oscillations are better adapted to the contextual memory processes that depend on this region of the brain (Davachi et al., 2003 and Davachi and Wagner, 2002). Frontally occurring fast spindles have also been previously linked to the consolidation of contextual information (van der Helm et al., 2011), as well as the suppression of memories that individuals are instructed to forget (Saletin et al., 2011). Nevertheless, despite these corroborative findings, it is important to note that we observed only marginal differences between the behavioural correlations with fast and slow spindles, meaning that further investigation of these spindle subtypes is warranted.

A suppressive influence of spindles on neutral contexts did not manifest in our group comparisons, as participants who napped after encoding exhibited less forgetting and more RT speeding for these items than those who remained awake. It is possible, however, that the source memory paradigm used in both the current study and our prior work (Lewis et al., 2011) was not sensitive enough to detect spindle-related contextual memory changes between conditions of post-learning wakefulness and either overnight or nap-based sleep. Evidence for a dynamic role of sleep spindles in selective memory processing may therefore be further established in future research through the use of behavioural tasks that adopt more sensitive assessments of contextual recall.

4.2. Contextual vs. central aspects of emotional memory

Across a series of experiments, Payne et al., 2012, Payne and Kensinger, 2011 and Payne et al., 2008 demonstrated that central emotional memory information and associated background details are differentially influenced by sleep. The task employed in these experiments was essentially the opposite of that used in the current study, with the emotional manipulation pertaining instead to a central object image that was either negative or neutral, and superimposed on a background image that was neutral in every instance. Notably, whereas Payne et al. (2012) revealed a sleep-dependent strengthening of memories for the negative objects, memories for the neutral backgrounds associated with these objects were weakened over sleep, suggesting that non-salient contextual information had been actively suppressed. Although sleep monitoring with PSG revealed a role for REM in consolidating negative objects, links between spindle activity and the processing of either central or contextual memory information over sleep were not addressed. As such, in terms of the properties of sleep that influence memories of emotional context, it is not possible to draw direct comparisons between Payne et al. and our current findings. Future research

should examine this topic further, and thereby deepen our understanding of the complex interactions between sleep, emotion and memory.

Acknowledgements

SAC was funded by the Engineering and Physical Sciences Research Council (EPSRC)(GR/T18806/01) and Unilever. PAL and SJD were funded by a Biotechnology and Biological Sciences Research Council (BBSRC) (BB/F003048/1) New Investigator Award to PAL. We are very grateful to both Andrew Mayes and Björn Rasch for critical reading of the manuscript and to two anonymous reviewers for their invaluable comments.

References

1.
 - Astori et al., 2013
 - S. Astori, R.D. Wimmer, A. Lüthi
 - Manipulating sleep spindles – expanding views on sleep, memory, and disease
 - Trends in Neurosciences, 36 (2013), pp. 738–748
2.
 - Baran et al., 2012
 - B. Baran, E.F. Pace-Schott, C. Ericson, R.M. C. Spencer
 - Processing of emotional reactivity and emotional memory over sleep
 - The Journal of Neuroscience, 32 (2012), pp. 1035–1042
3.
 - Born et al., 2006
 - J. Born, B. Rasch, S. Gais
 - Sleep to remember
 - The Neuroscientist, 12 (2006), pp. 410–424
4.
 - Born and Wilhelm, 2012
 - J. Born, I. Wilhelm
 - System consolidation of memory during sleep
 - Psychological Research, 76 (2012), pp. 192–203
5.
 - Cairney et al., 2014
 - S.A. Cairney, S.J. Durrant, J. Hulleman, P.A. Lewis
 - Targeted memory reactivation during slow wave sleep facilitates emotional memory consolidation
 - Sleep, 37 (2014), pp. 701–707
6.
 - Cairney et al., 2011
 - S.A. Cairney, S.J. Durrant, H. Musgrove, P.A. Lewis
 - Sleep and environmental context: interactive effects for memory
 - Experimental Brain Research, 214 (2011), pp. 83–92
7.
 - Cairney et al., in press
 - Cairney S.A., Durrant S.J., Power R. and Lewis P.A., Complementary roles of slow-wave sleep and rapid eye movement sleep in emotional memory consolidation, *Cerebral Cortex*, in press
8.
 - Clemens et al., 2005
 - Z. Clemens, D. Fabo, P. Halasz
 - Overnight verbal memory retention correlates with the number of sleep spindles

- Neuroscience, 132 (2005), pp. 529–535
- 9.
 - Dang-Vu et al., 2010
 - T.T. Dang-Vu, M. Schabus, M. Desseilles, V. Sterpenich, M. Bonjean, P. Maquet
 - Functional neuroimaging insights into the physiology of human sleep
 - Sleep, 33 (2010), pp. 1589–1603
- 10.
 - Davachi et al., 2003
 - L. Davachi, J.P. Mitchell, A.D. Wagner
 - Multiple routes to memory: distinct medial temporal lobe processes build item and source memories
 - Proceedings of the National Academy of Sciences of the United States of America, 100 (2003), pp. 2157–2162
- 11.
 - Davachi and Wagner, 2002
 - L. Davachi, A.D. Wagner
 - Hippocampal contributions to episodic encoding: insights from relational and item-based learning
 - Journal of Neurophysiology, 88 (2002), pp. 982–990
- 12.
 - De Gennaro and Ferrara, 2003
 - L. De Gennaro, M. Ferrara
 - Sleep spindles: an overview
 - Sleep Medicine Reviews, 7 (2003), pp. 423–440
- 13.
 - Deliens et al., 2013
 - G. Deliens, M. Gilson, R. Schmitz, P. Peigneux
 - Sleep unbinds memories from their emotional context
 - Cortex, 49 (2013), pp. 2221–2228
- 14.
 - Deliens et al., 2013
 - G. Deliens, D. Neu, P. Peigneux
 - Rapid eye movement sleep does not seem to unbind memories from their emotional context
 - Journal of Sleep Research, 22 (2013), pp. 656–662
- 15.
 - Deliens and Peigneux, 2013
 - G. Deliens, P. Peigneux
 - One night of sleep is insufficient to achieve sleep-to-forget emotional decontextualisation processes
 - Cognition and Emotion, 28 (2013), pp. 698–706
- 16.
 - Diekelmann, 2014
 - S. Diekelmann
 - Sleep for cognitive enhancement
 - *Frontiers in Systems Neuroscience*, 8 (2014) pp. 12. (Article number 46)
- 17.
 - Diekelmann and Born, 2010
 - S. Diekelmann, J. Born
 - The memory function of sleep
 - Nature Reviews: Neuroscience, 11 (2010), pp. 114–126
- 18.
 - Durrant et al., 2013

- S.J. Durrant, S.A. Cairney, P.A. Lewis
 - Overnight consolidation aids the transfer of statistical knowledge from the medial temporal lobe to the striatum
 - *Cerebral Cortex*, 23 (2013), pp. 2467–2478
- 19.
- Durrant et al., 2011
 - S.J. Durrant, C. Taylor, S. Cairney, P.A. Lewis
 - Sleep-dependent consolidation of statistical learning
 - *Neuropsychologia*, 49 (2011), pp. 1322–1331
- 20.
- Ellenbogen et al., 2006
 - J.M. Ellenbogen, J.D. Payne, R. Stickgold
 - The role of sleep in declarative memory consolidation: passive, permissive, active or none?
 - *Current Opinion in Neurobiology*, 16 (2006), pp. 716–722
- 1.
- Ferrarelli et al., 2007
 - F. Ferrarelli, R. Huber, M. Peterson, M. Massimini, M. Murphy, B. Riedner, A. Watson, P. Bria, G. Tononi
 - Reduced sleep spindle activity in schizophrenia patients
 - *The American Journal of Psychiatry*, 164 (2007), pp. 483–492
- 2.
- Gais et al., 2006
 - S. Gais, B. Lucas, J. Born
 - Sleep after learning aids memory recall
 - *Learning & Memory*, 13 (2006), pp. 259–262
- 3.
- Gais et al., 2002
 - S. Gais, M. Molle, K. Helms, J. Born
 - Learning-dependent increases in sleep spindle density
 - *The Journal of Neuroscience*, 22 (2002), pp. 6830–6834
- 4.
- Groch et al., 2013
 - S. Groch, I. Wilhelm, S. Diekelmann, J. Born
 - The role of REM sleep in the processing of emotional memories: evidence from behavior and event-related potentials
 - *Neurobiology of Learning and Memory*, 99 (2013), pp. 1–9
- 5.
- Hockley, 2008
 - W.E. Hockley
 - The effects of environmental context on recognition memory and claims of remembering
 - *Journal of Experimental Psychology. Learning, Memory, and Cognition*, 34 (2008), pp. 1412–1429
- 6.
- Hoddes et al., 1973
 - E. Hoddes, V. Zarcone, H. Smythe, R. Phillips, W.C. Dement
 - Quantification of sleepiness: a new approach
 - *Psychophysiology*, 10 (1973), pp. 431–436
- 7.
- Holland and Lewis, 2007
 - P. Holland, P.A. Lewis
 - Emotional memory: selective enhancement by sleep
 - *Current Biology*, 17 (2007), pp. R179–R181

8.
 - Hu et al., 2006
 - P. Hu, M. Stylos-Allan, M.P. Walker
 - Sleep facilitates consolidation of emotional declarative memory
 - *Psychological Science*, 17 (2006), pp. 891–898
9.
 - Intorini-Collison et al., 1996
 - I.B. Intorini-Collison, C. Dalmaz, J.L. McGaugh
 - Amygdala β -noradrenergic influences on memory storage involve cholinergic activation
 - *Neurobiology of Learning and Memory*, 65 (1996), pp. 57–64
10.
 - Kaestner et al., 2013
 - E.J. Kaestner, J.T. Wixted, S.C. Mednick
 - Pharmacologically increasing sleep spindles enhances recognition for negative and high-arousal memories
 - *Journal of Cognitive Neuroscience*, 25 (2013), pp. 1597–1610
11.
 - Lang et al., 2005
 - P.J. Lang, M.M. Bradley, B.N. Cuthbert
 - International affective picture system (IAPS): Affective ratings of pictures and instruction manual
 - (Technical Report A-6) *University of Florida, Gainesville, F.L.* (2005)
12.
 - Lau et al., 2010
 - H. Lau, M.A. Tucker, W. Fishbein
 - Daytime napping: effects on human direct associative and relational memory
 - *Neurobiology of Learning and Memory*, 93 (2010), pp. 554–560
13.
 - Lewis et al., 2011
 - P.A. Lewis, S. Cairney, L. Manning, H.D. Critchley
 - The impact of overnight consolidation upon memory for emotional and neutral encoding contexts
 - *Neuropsychologia*, 49 (2011), pp. 2619–2629
14.
 - Marrosu et al., 1995
 - F. Marrosu, C. Portas, M.S. Mascia, M.A. Casu, M. Fa, M. Giagheddu, A. Imperato, G.L. Gessa
 - Microdialysis measurement of cortical and hippocampal acetylcholine release during sleep-wake cycle in freely moving cats
 - *Brain Research*, 671 (1995), pp. 329–332
15.
 - Mednick et al., 2013
 - S.C. Mednick, E.A. McDevitt, J.K. Walsh, E. Wamsley, M. Paulus, J.C. Kanady, S.P. A. Drummond
 - The critical role of sleep spindles in hippocampal-dependent memory: a pharmacology study
 - *The Journal of Neuroscience*, 33 (2013), pp. 4494–4504
16.
 - Nishida et al., 2009
 - M. Nishida, J. Pearsall, R.L. Buckner, M.P. Walker
 - REM sleep, prefrontal theta, and the consolidation of human emotional memory
 - *Cerebral Cortex*, 19 (2009), pp. 1158–1166
- 17.

- Nishida and Walker, 2007
 - M. Nishida, M.P. Walker
 - Daytime naps, motor memory consolidation and regionally specific sleep spindles
 - PLoS One, 2 (2007), p. e341
- 18.
- Paller and Voss, 2004
 - K.A. Paller, J.L. Voss
 - Memory reactivation and consolidation during sleep
 - Learning & Memory, 11 (2004), pp. 664–670
- 19.
- Payne et al., 2012
 - J.D. Payne, A.M. Chambers, E.A. Kensinger
 - Sleep promotes lasting changes in selective memory for emotional scenes
 - Frontiers in Integrative Neuroscience, 6 (2012), p. 108
- 20.
- Payne and Kensinger, 2010
 - J.D. Payne, E.A. Kensinger
 - Sleep's role in the consolidation of emotional episodic memories
 - Current Directions in Psychological Science, 19 (2010), pp. 290–295
- 1.
- Payne and Kensinger, 2011
 - J.D. Payne, E.A. Kensinger
 - Sleep leads to changes in the emotional memory trace: evidence from fMRI
 - Journal of Cognitive Neuroscience, 23 (2011), pp. 1285–1297
- 2.
- Payne et al., 2008
 - J.D. Payne, R. Stickgold, K. Swanberg, E.A. Kensinger
 - Sleep preferentially enhances memory for emotional components of scenes
 - Psychological Science, 19 (2008), pp. 781–788
- 3.
- Plihal and Born, 1997
 - W. Plihal, J. Born
 - Effects of early and late nocturnal sleep on declarative and procedural memory
 - Journal of Cognitive Neuroscience, 9 (1997), pp. 534–547
- 4.
- Power and McGaugh, 2002
 - A.E. Power, J.L. McGaugh
 - Cholinergic activation of the basolateral amygdala regulates unlearned freezing behavior in rats
 - Behavioural Brain Research, 134 (2002), pp. 307–315
- 5.
- Rasch and Born, 2013
 - B. Rasch, J. Born
 - About sleep's role in memory
 - Physiological Reviews, 93 (2013), pp. 681–766
- 6.
- Rasch et al., 2007
 - B. Rasch, C. Buchel, S. Gais, J. Born
 - Odor cues during slow-wave sleep prompt declarative memory consolidation
 - Science, 315 (2007), pp. 1426–1429
- 7.
- Rechtschaffen and Kales, 1968
 - A. Rechtschaffen, A. Kales

- A manual of standardized terminology, techniques and scoring system for sleep stages of human subjects
 - U.S. Department of Health, Bethesda (MD) (1968)
- 8.
- Saletin et al., 2011
 - J.M. Saletin, A.N. Goldstein, M.P. Walker
 - The role of sleep in directed forgetting and remembering of human memories
 - *Cerebral Cortex*, 21 (2011), pp. 2534–2541
- 9.
- Schabus et al., 2007
 - M. Schabus, T.T. Dang-Vu, G. Albouy, E. Balteau, M. Boly, J. Carrier, A. Darsaud, C. Degueldre, M. Desseilles, S. Gais, C. Phillips, G. Rauchs, C. Schnakers, V. Sterpenich, G. Vandewalle, A. Luxen, P. Maquet
 - Hemodynamic cerebral correlates of sleep spindles during human non-rapid eye movement sleep
 - *Proceedings of the National Academy of Sciences of the United States of America*, 104 (2007), pp. 13164–13169
- 10.
- Schabus et al., 2004
 - M. Schabus, G. Gruber, S. Parapatics, C. Sauter, G. Klosch, P. Anderer, W. Klimesch, B. Saletu, J. Zeitlhofer
 - Sleep spindles and their significance for declarative memory consolidation
 - *Sleep*, 27 (2004), pp. 1479–1485
- 11.
- Schmidt et al., 2006
 - C. Schmidt, P. Peigneux, V. Muto, M. Schenkel, V. Knoblauch, M. Munch, D.J. de Quervain, A. Wirz-Justice, C. Cajochen
 - Encoding difficulty promotes postlearning changes in sleep spindle activity during napping
 - *The Journal of Neuroscience*, 26 (2006), pp. 8976–8982
- 12.
- Smith et al., 2005
 - A. Smith, R. Henson, M. Rugg, R. Dolan
 - Modulation of retrieval processing reflects accuracy of emotional source memory
 - *Learning & Memory*, 12 (2005), pp. 472–479
- 13.
- Smith et al., 2006
 - A.P. Smith, K.E. Stephan, M.D. Rugg, R.J. Dolan
 - Task and content modulate amygdala-hippocampal connectivity in emotional retrieval
 - *Neuron*, 49 (2006), pp. 631–638
- 14.
- Stickgold, 2005
 - R. Stickgold
 - Sleep-dependent memory consolidation
 - *Nature*, 437 (2005), pp. 1272–1278
- 15.
- Stickgold, 2013
 - R. Stickgold
 - Parsing the role of sleep in memory processing
 - *Current Opinion in Neurobiology*, 23 (2013), pp. 847–853
- 16.
- Stickgold and Walker, 2013
 - R. Stickgold, M.P. Walker

- Sleep-dependent memory triage: evolving generalization through selective processing
- Nature Neuroscience, 16 (2013), pp. 139–145
- 17.
 - Tamminen et al., 2010
 - J. Tamminen, J.D. Payne, R. Stickgold, E.J. Wamsley, M.G. Gaskell
 - Sleep spindle activity is associated with the integration of new memories and existing knowledge
 - The Journal of Neuroscience, 30 (2010), pp. 14356–14360
- 18.
 - Tucker et al., 2006
 - M.A. Tucker, Y. Hirota, E.J. Wamsley, H. Lau, A. Chaklader, W. Fishbein
 - A daytime nap containing solely non-REM sleep enhances declarative but not procedural memory
 - Neurobiology of Learning and Memory, 86 (2006), pp. 241–247
- 19.
 - van der Helm et al., 2011
 - E. van der Helm, N. Gujar, M. Nishida, M.P. Walker
 - Sleep-dependent facilitation of episodic memory details
 - PLoS One, 6 (2011), p. e27421
- 20.
 - Wagner et al., 2001
 - U. Wagner, S. Gais, J. Born
 - Emotional memory formation is enhanced across sleep intervals with high amounts of rapid eye movement sleep
 - Learning & Memory, 8 (2001), pp. 112–119
- 1.
 - Walker, 2008
 - M.P. Walker
 - Sleep-dependent memory processing
 - Harvard Review of Psychiatry, 16 (2008), pp. 287–298
- 2.
 - Walker, 2009
 - M.P. Walker
 - The role of sleep in cognition and emotion
 - Annals of the New York Academy of Sciences, 1156 (2009), pp. 168–197
- 3.
 - Walker and van der Helm, 2009
 - M.P. Walker, E. van der Helm
 - Overnight therapy? The role of sleep in emotional brain processing
 - Psychological Bulletin, 135 (2009), pp. 731–748
- 4.
 - Wamsley et al., 2010
 - E.J. Wamsley, M.A. Tucker, J.D. Payne, R. Stickgold
 - A brief nap is beneficial for human route-learning: the role of navigation experience and EEG spectral power
 - Learning & Memory, 17 (2010), pp. 332–336
- 5.
 - Wilhelm et al., 2008
 - I. Wilhelm, S. Diekelmann, J. Born
 - Sleep in children improves memory performance on declarative but not procedural tasks
 - Learning & Memory, 15 (2008), pp. 373–377
- 6.
 - Wilhelm et al., 2011

- I. Wilhelm, S. Diekelmann, I. Mozlow, A. Ayoub, M. Mölle, J. Born
- Sleep selectively enhances memory expected to be of future relevance
- The Journal of Neuroscience, 31 (2011), pp. 1563–1569
-

Corresponding author at: Department of Psychology, University of York, Heslington, York YO10 5DD, UK. Tel.: +44 1904 324 355; fax: +44 1904 433 181.

Copyright © 2014 Published by Elsevier Ltd.
