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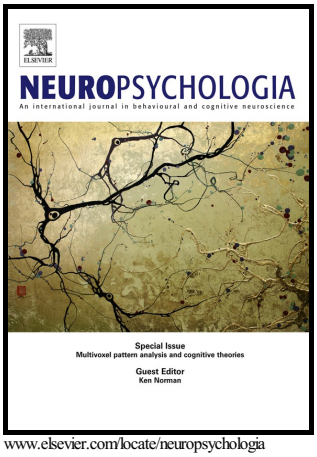

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Lateralised sleep spindles relate to false memory generation

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Abstract

Sleep is known to enhance false memories: After presenting participants with lists of semantically related words, sleeping before recalling these words results in a greater acceptance of unseen "lure" words related in theme to previously seen words. Furthermore, the right hemisphere (RH) seems to be more prone to false memories than the left hemisphere (LH). In the current study, we investigated the sleep architecture associated with these false memory and lateralisation effects in a nap study. Participants viewed lists of related words, then stayed awake or slept for approximately 90 minutes, and were then tested for recognition of previously seen-old, unseen-new, or unseen-lure words presented either to the LH or RH. Sleep increased acceptance of unseen-lure words as previously seen compared to the wake group, particularly for RH presentations of word lists. RH lateralised stage 2 sleep spindle density relative to the LH correlated with this increase in false memories, suggesting that RH sleep spindles enhanced false memories in the RH.

Keywords

Sleep spindles, memory, false memory, sleep consolidation, hemispheric lateralisation

1. Introduction

Sleep has a profound impact on the consolidation of new memories. Contemporary models of memory consolidation suggest that during sleep memories are repeatedly reactivated in hippocampal networks (Rasch, Büchel, Gais, & Born, 2007; Rudoy,

Voss, Westerberg, & Paller, 2009), with this reactivation gradually leading to plastic synaptic changes within neocortical networks, thus consolidating the memory. Furthermore, different sleep stages have been found to have different influences on this process. For instance, slow-wave sleep (SWS) has been found to be beneficial for declarative memory consolidation (cf. Diekelmann & Born, 2010; Marshall & Born, 2007), whilst NREM stage 2 has been linked to both declarative (Gais, Mölle, Helms, & Born, 2002; Genzel, Dresler, Wehrle, Grözinger, & Steiger, 2009; Ruch et al, 2012; van der Helm, Gujar, Nishida, & Walker, 2011), and procedural-motor task consolidation (Fogel & Smith, 2006; Fogel, Smith, & Cote, 2007; Nishida & Walker, 2007).

Sleep spindles have also been directly related to memory consolidation. Considered a characteristic feature of stage 2 sleep, but also present during SWS, spindles (10 -16 Hz oscillations lasting up to 3s) are thalamocortical oscillations that are implicated in offline information processing for both declarative and procedural learning (Clemens, Fabo, & Halasz, 2005; Cox, Hofman, & Talamini, 2012; Gais et al., 2002; Nishida & Walker, 2007; Ruch et al., 2012; Schabus et al., 2004, 2008; Tamaki, Matsuoka, Nittono, & Hori., 2008; Tamminen, Payne, Stickgold, Wamsley, & Gaskell, 2010; van der Helm, Gujar, Nishida, & Walker, 2011), and have been interpreted in terms of information transfer from hippocampus to neocortex (Diekelmann & Born, 2010; Rasch & Born, 2013). Moreover, different types of spindle have been identified. Fast spindles (13-15Hz) largely occur during stage 2 sleep and are focused around the centro-parietal region, and have been linked to hippocampal activity suggesting a role in memory consolidation (Diekelmann & Born, 2010; Girardeau, Benchenane, Wiener, Buzsaki, & Zugaro, 2009; van der Helm et al., 2011). Slow spindles (10-12Hz) are primarily observed in frontal areas and although are present during stage 2, are more commonly associated with SWS. For integration of vocabulary with long-term store, Tamminen, Lambon Ralph, and Lewis (2013) observed that *lateralised* LH spindle activity was predictive of degree of integration of new words in semantic memory. These results are consistent with the

theory that sleep aids integration of recent experiences into the long-term vocabulary store (Dumay & Gaskell, 2007, 2012) which is primarily located in the LH (Ellis et al., 2009; Tamminen et al., 2010).

However, sleep effects on memory are not only limited to veridical memory, with recent studies demonstrating that sleep is also important for abstraction and extraction of "gist", or the common theme, from sets of information (Durrant & Lewis, 2009; Fischer, Drosopoulos, Tsen, & Born, 2006; Gomez, Bootzin, & Nadel, 2006), as well as enabling integration of information from multiple memories (Ellenbogen, Hu, Payne, Titone, & Walker, 2007; Tamminen, Payne, Stickgold, Wamsley, & Gaskell, 2010), and allowing extraction of proto-rules and themes from newly encoded memories (Nadel, Hupbach, Gomez, & Newman-Smith, 2012; Nere, Hashmi, Cirelli, & Tononi, 2013).

Sleep can also affect generation of false memories for information that had not been previously experienced (Diekelmann, Born, & Wagner, 2010; Pardilla-Delgado & Payne, 2017; Payne et al., 2009). In the field of false memory research, the most common form of test uses the Deese-Roediger-McDermott (DRM, Deese, 1959; Roediger & McDermott, 1995) paradigm that exposes participants to lists of semantically related words (e.g., *bed, rest, awake, tired, dream, wake, snooze, nap, snore*), and then tests recall or recognition of words that are part of the list (seen-old), not related to the list (unseen-new), or not previously seen but related to the theme of the list (unseen-lure words, e.g., for the above examples, *sleep*). Participants are more likely to accept as previously seen the unseen-lure rather than the unseen-new words (McDermott, 1996; Roediger, Watson, McDermott, & Gallo, 2001; Stadler, Roediger, & McDermott, 1999; Underwood, 1965).

Payne et al. (2009) linked false memory effects to different sleep stages, and found a negative correlation between time spent in SWS and recall accuracy in both overnight and nap studies, indicating that SWS promoted false memories. Pardilla-Delgado and Payne (2017) performed a similar study but with both a recall and a recognition task. Though there was no significant correlation between SWS and

recall accuracy, they observed a significant negative correlation between SWS and false memory recognition, with the authors suggesting this was due to SWS supporting consolidation of contextual and episodic details of the DRM lists increasing the ability to discriminate between presented and non-presented words, akin to source-monitoring that has been shown to decrease false recognition (Neuschatz, Benoit, & Payne, 2003). Lutz, Diekelmann, Hinse-Stern, Born, and Rauss (2017) found that a single night of sleep increased veridical memory, but multiple nights of sleep contributed to extraction of gist from visually presented sets of items in the DRM paradigm.

There are numerous studies demonstrating the beneficial influence of SWS on consolidation of veridical episodic and declarative memory (cf. Diekelmann & Born, 2010; Marshall & Born, 2007; Peigneux et al., 2004; Takashima et al., 2006), but also increased abstraction and gist extraction of memory (Gomez et al., 2006; Fischer et al., 2006, Lewis & Durrant, 2011), and gist extraction could be a plausible explanation for this false memory generation and the negative correlation between SWS and recall accuracy. False memory effects could be due to extraction of a central theme, or gist, from a set of related information which then prompts acceptance of an unseen-lure word (due to abstraction and extraction of a gist from a set of related information, which then prompts acceptance of an unseen-lure word (Brainerd & Reyna, 2005). Lewis and Durrant (2011) propose a theoretical model to account for these effects of gist extraction associated with sleep. The "information Overlap to Abstract" (iOtA) model proposes that gist extraction occurs alongside memory consolidation, where overlapping replay of related memories during sleep preferentially strengthens the shared elements of a set of information, such as an unseen lure word from a thematically related list of words. Alternatively, it may be that broader associations in long-term semantic memory in the neocortex are more active during sleep (Cai, Mednick, Harrison, Kanady, & Mednick, 2009; Sio, Monaghan, & Ormerod, 2013) which could contribute to increased false memories as more distant associates to the seen words, including unseen-lure words (Roediger,

Watson, McDermott, & Gallo, 2001) would then be activated (Howe, Wilkinson, & Monaghan, 2012).

Whereas Payne et al. (2009) demonstrated the role of SWS in false memory formation, and despite their role in hippocampal to neocortical transfer, there have been no previous studies of the role of sleep spindles in false memories. The first aim of our study was to determine how sleep spindles related to consolidation of veridical and false memories in the DRM paradigm. In accordance with previous studies indicating that sleep spindle density relates to consolidation of recent experience with long-term memory (e.g., Tamminem et al., 2013), we predicted that LH lateralised sleep spindle density would relate to veridical memory for the DRM task as this would promote alignment of words seen with their long-term representation in the vocabulary store.

However, the role of the RH in veridical and false memory and the effect of sleep on its processing are understudied. Both the LH and RH are capable of processing words (Marsolek & Deason, 2007; Shillcock, Ellison, & Monaghan, 2000), but do so with different signatures in terms of semantic processing effects. Distantly associated words prime one another in the RH, whereas only closely associated words are primed in the LH, which indicates that the LH semantic associative network prioritises a small network of strongly-associated words whereas the RH activates a broader network of more weakly-associated words (Beeman, 1998; Beeman & Bowman, 2000; Monaghan, Shillcock, & McDonald, 2004), analogous to coarse- and fine- coding asymmetries seen in visual processing between the two hemispheres (Brady, Campbell, & Flaherty, 2005; Christman, Kitterle, & Hellige, 1991; Hsiao, Cipollini, & Cottrell, 2013; Monaghan & Shillcock, 2004). It has previously been observed that more false memories for DRM lists occur when words are presented to the RH rather than the LH at retrieval (Bellamy & Shillcock, 2007; Faust, Ben-Artzi, & Harel, 2008; Ito, 2001; Westerberg & Marsolek, 2003).

Furthermore, during overnight sleep, there is greater activity in the RH than the LH in the early half of the night (Casagrande & Bertini, 2008a, 2008b; Natale et

al., 2007, 2010) indicating potential for asymmetries in the effect of sleep on memory to occur. Monaghan, Shaw, Ashworth-Lord, and Newbury (2017) tested behaviourally the effect of overnight sleep on lateralised memory by presenting DRM stimuli to the LH or RH at retrieval. They replicated studies finding that sleep facilitated false memories, and further demonstrated a differential effect of sleep on LH versus RH recognition accuracy, with sleep promoting accuracy in the LH compared to the RH, whereas the wake group showed an advantage for accuracy in the RH compared to the LH. These results were interpreted as sleep primarily affecting access to veridical memory in the LH, thus opening up the possibility that the RH is key for generation of false memories, either by sleep promoting gist extraction in the RH or by increasing spreading activation in the broader associative network in the RH thereby increasing activation of unseen lure words during testing.

In the current study we extended the behavioural study of Monaghan et al. (2017), which demonstrated a lateralised effect of memory retrieval for DRM word lists, by using a nap study paradigm where we measured the relationship between sleep architecture and construction of false memories. We hypothesised that the key effects of sleep-enhanced false memory would be reproduced in our study. We also predicted that, if the RH is dominant in false memory generation then we should observe enhanced false memories (greater acceptance of unseen lure words) in the RH compared to the LH associated with sleep. Furthermore, if sleep affects veridical memory consolidation then we should observe increased acceptance of seen old words in the LH than the RH associated with sleep. In terms of sleep architecture, we predicted that sleep spindles will contribute to generation of representations of previously experienced words (Tamminem et al., 2013) with LH involved in veridical memory, and in addition predicted that sleep spindles in the RH may involve consolidation with the broader semantic associative network, resulting in enhanced gist extraction or greater activation of distantly related associates.

2. Method

2.1. Participants

32 healthy, medication free university students (26 females; mean age = 19.72, SE = .30) were paid £21 for participating. Participants maintained a normal sleep schedule for two days prior to testing as reported by sleep diaries, were asked to sleep at least 8 hours for the night preceding the study, and abstain from alcohol and caffeine based products for 12 hours preceding the study. All participants were right-handed as assessed by the Oldfield Handedness questionnaire (1971). This research was approved by the University Research Ethics Committee.

2.2. Materials

For the memory task a total of 12 word lists were taken from Stadler et al. (1999). Each list contained 10 words associated with a semantic topic, along with an associated unseen-lure word which related to the theme of the word list (the list themes were: *car, chair, doctor, bread, fruit, sleep, thief, river, needle, music, mountain, king*). For testing, 48 words comprising 12 unseen-lure words, 24 seen-old words (two previously seen-old words from each word list), and 12 unrelated unseen-new words taken from other unused DRM word lists in Stadler et al. (1999) were used. All words were presented in lower case Courier New bold, black, 18 point font on a computer screen. In the training task words were presented centrally to avoid any potential hemispheric bias at encoding. During the recognition task lateralised presentations of words were positioned with the near edge of the word 2.9° either to the left or right of the fixation point and subtending between 2.9° and 4.5° of the visual field depending on the word's length. In total 12 seen-old, 6 unseen-lure, and 6 unseen-new words were presented to each hemisphere.

2.3. Procedure

Participants arrived at the sleep lab at 11:30h and were attached with the polysomnography equipment regardless of group, in order to prevent any confounds that may arise from expectations about the study conditions. At approximately

12:00h they participated in the exposure phase of the memory task. Participants sat 60cm from a computer screen that displayed a central fixation point for 500ms followed by a word presented horizontally in the centre of the screen for 1500ms. After viewing all the words from one list of thematically related words they completed maths problems as a distractor task for 30 s before moving onto the next list. The process was repeated until all 12 word lists had been seen. The word list order, and order of words within each list, was randomised.

Participants were then randomly assigned into a sleep or wake group. Those in the sleep group were monitored with polysomnography (PSG), recorded with an Embla N7000 system using EEG sites O1, O2, C3, C4, F3, and F4 referenced against the contralateral mastoid (M1 and M2). All signals were digitally sampled at a rate of 200 Hz and verified at the beginning and the end of the study to have a connection impedance of <5kΩ, with any noisy channels removed from analysis. Sleep participants had the opportunity to sleep from 12:15h until 14:00h, whereas those in the wake group watched an emotionally neutral movie with no verbal stimuli (a Mr Bean cartoon or a nature documentary) with neutral music played over for the same duration and were monitored to ensure they remained awake. At 14:00 those in the sleep group were woken and were given the opportunity to remove sensors and have a short break to prevent any potential effects of sleep inertia before completing the recognition task.

At 14:15h the memory recognition phase began. Participants were again sat 60cm from the computer screen, and were instructed to press a yes or no key according to whether they had previously seen a word appearing on a computer screen or not. At the start of each trial a central fixation point appeared in the screen for 500ms, which participants were instructed to focus on, followed by a word presented to the left or right hemisphere for 120ms. The unseen-lure words, seen-old words, and unseen-new words were assigned equally to the right or left hemisphere presentation and were presented in random order. Once all 48 test words were presented, the study was finished. Viewing location was not recorded,

which was a limitation of our study. However, participants show excellent conformity with fixation instructions, with 97% of fixations at the requested location in lateralisation studies for word presentations (Whitney & Lavidor, 2004).

Sleep data were scored in 30s epochs independently by two sleep researchers in accordance with the standardised sleep scoring criteria of Rechtschaffen and Kales (1968). For spindle analysis, as spindles mainly emerge over the frontal-centro and centro-parietal areas, only electrodes positioned in these locations were analysed. Spindle analysis involved NREM (stage 2 and slow wave sleep) band-pass filtered (11-15Hz) using a linear finite impulse response filter, with the range selected based on Tamminen et al. (2013). Using an automated detection algorithm (Ferrarelli et al., 2007) we derived the number of discrete spindle effects for each channel, with amplitude fluctuations in the filtered time series exceeding a predetermined threshold counted as spindles. Thresholds were calculated relative to mean channel amplitude (eight times average amplitude).

As slow and fast frequency spindles may relate to distinct memory consolidation processes (Mölle, Bergmann, Marshall, & Born, 2011; van der Helm et al., 2011), spindles were filtered for slow (11-13Hz) and fast (13-15Hz) sleep spindles, with the frequency range consistent with Ferrarelli et al. (2007), Tamminen et al. (2013), and van der Helm et al. (2011).

3. Results

3.1 Statistical Analysis

Criteria for including participants for analysis were participants reporting more than 6 hours sleep per night in the 3 nights leading up to the study and sleeping in the study for more than 50 minutes within the sleep condition, and all participants passed these criteria. We first tested whether previously observed behavioural effects of overnight sleep on memory for words were reproduced here in a nap study, determining (1) whether there was an overall false memory effect, i.e., greater unseen-lure word than unseen-new word acceptance; (2) whether this false

memory effect was enhanced by sleep (Payne et al., 2009); and (3) whether the dominance of veridical memory of studied words in the LH was a consequence of sleep (Monaghan et al., 2017). We conducted a 3-way mixed ANOVA with response accuracy in terms of proportion of words recognised as old as the dependent variable, group (sleep or wake) as between subjects factor, and hemisphere (LH, RH) and word type (unseen-lure, unseen-new, seen-old) as within subjects factors. See Table 1 for the descriptive statistics. As each word type represents a different measure of memory (i.e., hits in seen-old, false alarms in unseen-new, and false memories in unseen-lure), we also performed ANOVAs for each word type separately, as in previous studies of false memory and sleep (see Diekelmann et al., 2008, 2010; Fenn et al., 2009).

After these ANOVAs, we then determined the relation between the significant memory effects associated with sleep and measures of sleep architecture, including sleep spindles. In these analyses, significance values were initially corrected for multiple comparisons between each sleep stage and sleep spindles and memory tests (correction was for 12 tests initially). Follow-up correlations had significance values corrected within sets of comparisons.

Finally, we verified whether observations of veridical and false memories from the recognition rates for each word type separately were verified by signal detection analyses were applied to the data. It may be the case that effects of sleep on false memories, for instance, are a consequence of changes in discriminability to memory of these words, or it may be that sleep affects the response bias of participants to accept more words as old. To address this, we conducted analyses of true and false recognition rates according to the non-parametric signal detection measures *A′* (sensitivity) and B″ (response bias) (Boice & Gardner, 1988; Donaldson, 1992; Snodgrass & Corwin, 1988) as used in Pardilla-Delgado and Payne (2017) for analysing effects of delay between encoding and recognition on false memories. We distinguished measures of true recognition (distinguishing between old-seen and old-unseen words), and false recognition (distinguishing between old-lure and old-

unseen words), computed separately for the LH and the RH, where the formulae were as follows (where H is seen-old hit rate, FAF is unseen-new false recognition, and FAC is unseen-lure false recognition):

True recognition: A' = .5 + ((H - FAF)(1 + H - FAF)) / (4H(1 - FAF)) assuming H ≥ FAF, and A' = 0.5 + ((FAF - H)(1 + FAF - H)) / (4FAF(1 - H)) assuming FAF > H. B" = (H(1 - H) – FAF(1 – FAF))/(H(1 – H) + FAF(1 – FAF)) when H ≥ FAF, and (FAF(1 - FAF) – H(1 – H))/(FAF(1 – FAF) + H(1 – H)) when FAF > H.

False recognition: A' = .5 + ((FAC - FAF)(1 + FAC - FAF)) / (4FAC(1 - FAF)) assuming FAC ≥ FAF, and A' = 0.5 + ((FAF - FAC)(1 + FAF - FAC)) / (4FAF(1 - FAC)) assuming FAF > FAC. B" = (FAC(1 - FAC) – FAF(1 – FAF))/(FAC(1 – FAC) + FAF(1 – FAF)) when FAC ≥ FAF, and (FAF(1 - FAF) – FAC(1 – FAC))/(FAF(1 – FAF) + FAC(1 – FAC)) when FAF > FAC.

3.2 Recognition rate by word type

There were no significant main effects of sleep or wake group, $F(1, 30) = 1.296$, $p = .264$, $\eta_p^2 = .041$, or hemisphere, $F < 1$, but there was a main effect of word type, $F(2, 60) = 59.674$, $p < .001$, $\eta_p^2 = .665$, demonstrating the standard false memory effect, with unseen-new words (M = .224, SE = .025) resulting in significantly fewer false recognitions than unseen-lure words (M = .680, SE = .025, $p < .001$) which were recognised as old words not significantly different than seen-old words (M = .609, SE = .025, $p = .100$).

Table 1. Proportion identified as 'Seen-Old' (SE in parentheses) for each word type, by hemisphere, and sleep or wake group. (LVF- Left Visual Field, RH- Right Hemisphere, RVF- Right Visual Field, LH- Left Hemisphere).

Word Type	Sleep		Wake	
	LVF/RH	RVF/LH	LVF/RH	RVF/LH
Seen-Old	.621 (.045)	.678 (.034)	.559 (.045)	.577 (.034)
Unseen-New	.229 (.057)	.125 (.059)	.282 (.057)	.261 (.059)
Unseen-Lure	.802 (.057)	.677 (.049)	.572 (.057)	.667 (.049)

Also as predicted, there was a significant word type by group interaction, $F(2, 60) = 3.229$, $p = .047$, $\eta_p^2 = .097$. Simple main effects analyses revealed this was due to the wake group (M = .619, SE = .046) identifying fewer lure words as previously appearing than the sleep group (M = .759, SE = .037), $F(1, 30) = 5.438$, $p = .025$ $\eta_p^2 = .156$, again replicating previous observations of sleep increasing false memories. There were no significant differences in unseen-new, $F(1, 30) = 1.544$, $p = .224$ $\eta_p^2 = .049$, or seen-old, $F(1, 30) = 3.433$, $p = .074$ $\eta_p^2 = .103$, word recognition rates between the wake and sleep groups (see Figure 1). There was no significant hemisphere by group interaction, $F(1, 30) = 3.497$, $p = .071$, $\eta_p^2 = .104$, or hemisphere by word type interaction, $F(1, 30) = 1.741$, $p = .184$, $\eta_p^2 = .055$.

There was also a marginally significant 3-way interaction between hemisphere, word type, and group, $F(2,60) = 2.867$, $p = .065$, $\eta_p^2 = .087$. As previous studies have conducted analyses separately for each word type and revealed sleep-specific effects on false memories (Diekelmann et al., 2008, 2010; Fenn et al., 2009), we also performed these separate analyses in order to examine the effect of sleep on each word type. Unseen-lure words showed no significant effect of hemisphere, $F < 1$, but a significant effect of group, $F(1, 30) = 5.142$, $p = .027$, $\eta_p^2 = .114$, with the sleep group significantly more likely to identify unseen-lure words as old (M =. 740, SE = .037) compared to the wake group (M = .620, SE = .037). There was also a significant hemisphere by group interaction, $F(1, 30) = 4.321$, $p = .016$, $\eta_p^2 = .179$. Further post-hoc analysis revealed this interaction came from a non-significant difference in the LH between sleep (M = .677, SE = .053) and wake groups (M = .667, SE = .053), $F < 1$, but a significant difference in the RH between sleep (M = .803, SE = .053), and wake group (M = .573, SE = .053), $F(1, 30)= 8.169$, $p = .008$, $\eta_p^2 = .214$, suggesting that sleep led to a significant increase in RH unseen-lure word acceptance, but no difference in the LH. The difference between RH and LH recognition was not significant in either the sleep group, $F(1, 15)= 4.442$, $p = .053$, $\eta_p^2 = .228$, or the wake group, $F(1, 15) = 2.312$, $p = .149$, $\eta_p^2 = .134$.

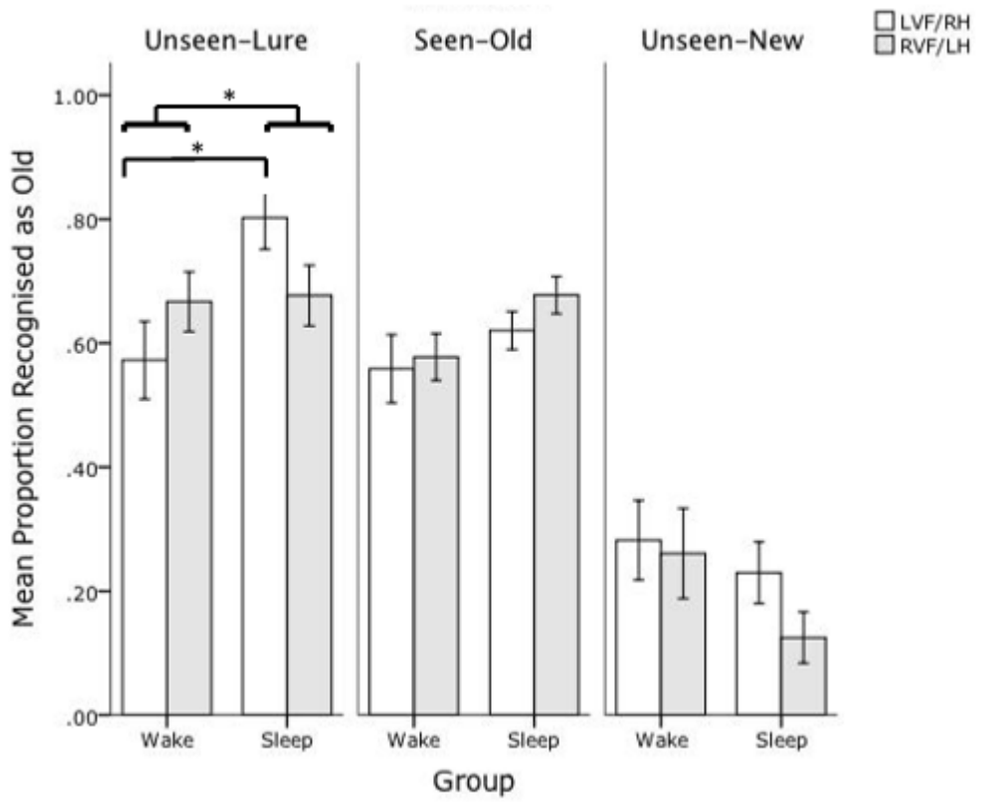

Figure 1. Proportion of words endorsed as 'Old' by word type for sleep and wake groups by hemisphere. Error bars show ± 1 SEM. LVF- Left Visual Field, RH- Right Hemisphere, RVF- Right Visual Field, LH- Left Hemisphere

For unseen-new words, as expected there was no significant difference between group, $F(1, 30) = 1.676$, $p = .205$, $\eta_p^2 = .053$, hemisphere, $F(1, 30) = 2.567$, $p = .120$, $\eta_p^2 = .079$, or a group by hemisphere interaction, $F < 1$. For seen-old words there was no significant effect of group, $F(1, 30) = 3.433$, $p = .078$, $\eta_p^2 = .100$, hemisphere, $F(1, 30) = 1.201$, $p = .282$, $\eta_p^2 = .038$ or a group by hemisphere interaction, both $F < 1$.

3.3 Sleep stage effects

We measured total sleep time, time spent in stage 1, stage 2, SWS, and REM for the sleep group (see Table 2). We then correlated proportion of time in each sleep stage with memory accuracy for each word type, separately for LH and RH as well as averaged over the two hemispheres, to determine whether false or studied words were affected by particular sleep stages. REM sleep was excluded from further

analysis as only two participants had entered that stage. Proportion of sleep time was used to control for total sleep time between participants. There were no significant correlations between proportion of any sleep stage and accuracy (See Table 3). Correlations between total sleep time and memory accuracy measures were similar.

Table 2. Mean duration stage 1, stage 2, SWS, and REM sleep in minutes ± 1 SEM.

Sleep Stage	Minutes ± SEM
Total Sleep Time	69.46 ± 3.65
Stage 1	16.93 ± 1.88
Stage 2	29.75 ± 2.28
SWS	20.68 ± 2.39
REM	2.09 ± .65
Average Wake after Sleep Onset	17.9 ± 2.08
Average Sleep Onset Latency	12.53 ± 2.03

Table 3. Correlation coefficients between recognition accuracy, and proportion of total time slept in each sleep stage.

	Unseen-new Word Recognition	Unseen-lure Word Recognition	Seen-old Word Recognition	LH Accuracy	RH Accuracy
Stage 1	-.121	-.141	.151	.019	-.173
Stage 2	-.216	-.149	-.029	-.083	-.242
SWS	.083	.290	-.162	-.066	.285

For the sleep spindle analysis, as spindles in different sleep stages have been demonstrated to have distinct effects on memory (Cox et al., 2012), spindles were measured in both stage 2 and SWS separately. In order to control for variability between participants in total time in each sleep stage, spindle-per-minute density was measured for each individual electrode site. The difference between LH and RH spindle density was computed to determine the lateralisation effects of spindles in adjacent electrode sites (C3-C4, F3-F4) in order to determine lateralised spindles when controlled for overall spindle density, which varies between participants and can be related to other performance characteristics (such as IQ, Schabus et al., 2006; Ujma, Sandor, Szakadat, Gombos, & Bodizs, 2016). We refer to the difference

between LH and RH sleep spindle density in terms of lateralisation of spindles, which describes a relative lateralisation in terms of imbalance between spindles in the LH and the RH.

3.3.1 Stage 2 sleep spindles

In these analyses, we focused on unseen-lure word recognition as this was the key effect in the behavioural results. There was a significant correlation between unseen-lure false recognition and C3-C4 stage 2 spindle density, r = -.748, p = .004 (corrected), see Figure 2 indicating that false memories increased as lateralisation of spindles to the RH increased. Distinguishing between performance in the LH and the RH demonstrated a significant correlation between C3-C4 stage 2 spindle density and LH unseen-lure recognition accuracy, r = -.593, p = .015, (p = .045 corrected), but not between C3-C4 stage 2 spindle density and RH unseen-lure recognition accuracy, r = -.471, p = .066, uncorrected), though in each case the lateralisation effects were similar: greater RH compared to LH spindle density resulted in greater false memories.

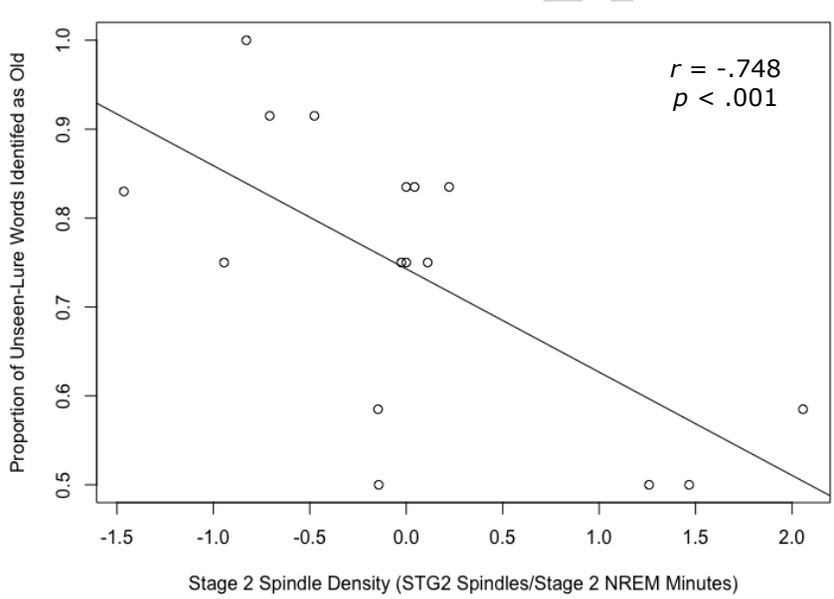

Figure 2. Correlation between lateralised spindle density (C3-C4) by unseen-lure recognition accuracy.

For F3-F4 stage 2 sleep spindle density, there was no significant correlation between unseen-lure recognition accuracy and F3-F4, r = -.066, p = .808, nor for

LH unseen-lure recognition accuracy, r = -.153, p = .572, or RH unseen-lure recognition accuracy, r = .009, p = .973, with F3-F4.

In order to determine whether density of spindles within each hemisphere, rather than the lateralised density measure was driving the memory effects, further correlations were conducted with individual electrode site (C3, C4, F3, F4) stage 2 spindle densities (see Table 4). None of the correlations were significant. Distinguishing between LH and RH unseen lure false recognition also resulted in no significant correlations, after corrections for multiple comparisons (see Table 4). These results indicated that the critical effect on lure word recognition was due to differences in spindle density measured across sites C3 and C4.

Table 4. Correlation coefficients between overall, LH and RH unseen lure false recognition with individual electrode sleep spindle density in sleep stage 2.

	Overall Unseen-Lure Word Recognition	LH Unseen-Lure Word Recognition	RH Unseen-Lure Word Recognition
C3	-.477	-.561*	.012
C4	-.083	-.262	.283
F3	-.417	-.204	-.168
F4	-.334	-.082	-.159

* p = .024 uncorrected, p = .288 corrected.

Further correlations were also conducted between the lateralised spindle measures (C3-C4, F3-F4) and seen-old word recognition and unseen-new word recognition. None of the correlations were significant (See Table 5). Hence, the correlations with sleep spindles were only found for the significant behavioural changes in memory performance.

Table 5. Correlation coefficients between seen-old and unseen-new recognition with lateralised sleep spindle density in sleep stage 2.

	Seen-Old Word Recognition	Unseen-New Word Recogniton
C3-C4	-.343	-.067

F3-F4	.222	-.162

3.3.2 SWS Sleep spindles

In order to see if the spindle correlations were specific to stage 2, correlations were conducted between lateralised SWS spindle density (C3-C4, F3-F4) and overall unseen-lure word recognition, LH unseen-lure word recognition, and RH unseen-lure word recognition. None were significant, all $r < .321$, $p > .226$. Correlations between individual electrode sites (C3, C4, F3, F4) and overall unseen-lure word recognition, LH unseen-lure word recognition, and RH unseen-lure word recognition were also all non-significant, all $r < .372$, $p > .156$.

3.3.3 Slow and fast sleep spindles

To determine whether differences between C3 and C4 spindle density relating to the memory effects were due to slow or fast spindles, we correlated C3-C4 spindle density with the slow (11-13Hz) and fast (13-15Hz) filters applied, and correlated with overall unseen-lure recognition, LH unseen-lure recognition, and RH unseen-lure recognition.

For slow spindles, there were no significant correlations between C3-C4 and overall unseen-lure recognition accuracy, $r = -.198$, $p = .463$, LH unseen lure recognition accuracy, $r = .038$, $p = .888$, or RH unseen lure recognition accuracy, $r = -.273$, $p = .306$. However, for fast spindles, there was a significant correlation between C3-C4 and overall unseen-lure recognition accuracy, $r = -.619$, $p = .011$, but no significant correlation with LH unseen lure recognition accuracy, $r = -.446$, $p = .083$, or RH unseen lure recognition accuracy, $r = -.469$, $p = .067$. These results suggest that fast rather than slow sleep spindles were driving the observed memory effects.

3.4 Signal detection analyses

Signal detection analyses enable distinctions between whether the observations of sleep effects for accuracy of unseen lure word recognition were due

to changes in sensitivity, or whether they could be accounted for by changes in response bias as a consequence of sleep. Table 6 reports the descriptive statistics for the measures of A' (discriminability) and B'' (response bias) by group and hemisphere for true recognition (responding differently to old compared to new unrelated words) and for false recognition (responding differently to lure compared to new unrelated words). We conducted ANOVAs on A' and B'' measures separately, with group (sleep, wake), hemisphere (RH, LH) and memory type (true recognition, false recognition) as factors. We first investigated the three-way interaction, then, unpacked this due to the sleep effect on different memory types across the hemispheres.

Table 6. Discriminability as measured by *A'* (SE in parentheses) and response bias as measured by *B'* (SE in parentheses) by memory type, hemisphere, and group. (LVF- Left Visual Field, RH- Right Hemisphere, RVF- Right Visual Field, LH- Left Hemisphere).

Word Type	Sleep		Wake	
	LVF/RH	RVF/LH	LVF/RH	RVF/LH
True Recognition A'	.784 (.025)	.862 (.027)	.816 (.025)	.797 (.027)
False Recognition A'	.867 (.029)	.849 (.028)	.779 (.029)	.841 (.028)
True Recognition B''	.263 (.107)	.574 (.139)	.368 (.107)	.348 (.139)
False Recognition B''	-.215 (.163)	.463 (.160)	.268 (.163)	.194 (.160)

For A', there was a significant 3-way interaction between group, hemisphere, and true or false recognition memory, $F(1, 30) = 17.353$, $p < .001$, $\eta_p^2 = .366$ (see Figure 3). When split by group, in the sleep group there was a significant interaction between hemisphere and memory type, $F(1, 15) = 10.859$, $p = .005$, $\eta_p^2 = .420$. Post-hoc analysis revealed this to be due to greater discriminability for false recognition than true recognition (i.e., greater false memory effects) in the RH, $F(1, 15) = 9.930$, $p = .007$, $\eta_p^2 = .398$, but no difference within the LH, $F < 1$. For the wake group, there was again a significant hemisphere by memory type interaction, $F(1, 15) = 6.868$, $p = .019$, $\eta_p^2 = .314$. Post hoc analysis demonstrated that true

recognition was lower in discriminability than false recognition in the LH, $F(1, 15) = 4.895$, $p = .043$, $\eta_p^2 = .246$, but no difference in the RH, $F(1, 15) = 1.539$, $p = .234$, $\eta_p^2 = .093$. These results for the sleep group confirmed the analyses of the word types, demonstrating that lateralised false memory effects were due to changes in discriminability associated with sleep. The effect of increased discriminability for false over true recognition in the LH for the wake group was unexpected, but consistent with sleep increasing lateralisation of false memories to the RH.

For the ANOVA on B'', there was a significant 3-way interaction between hemisphere, memory type, and group, $F(1, 30) = 4.571$, $p = .041$, $\eta_p^2 = .132$. When split by group, for the sleep group there was a memory type by hemisphere interaction, $F(1, 15) = 5.161$, $p = .038$, $\eta_p^2 = .256$. Post hoc analyses demonstrated that judgments were more conservative for true than false recognition in the RH, $F(1, 15) = 10.848$, $p = .005$, but no difference in the LH, $F(1, 15) = 1.491$, $p = .241$. For the wake group, there was no significant interaction between memory type and hemisphere, $F < 1$. These results demonstrated that sleep affected response bias as well as discriminability in the RH, particularly for false recognition.

4. Discussion

Within the current study we had two main objectives. First, we aimed to replicate previous effects of sleep increasing false memory effects for words (Diekelmann et al., 2010; Pardilla-Delgado & Payne, 2017; Payne et al., 2009), as well as the interaction of these false memory sleep effects with hemispheric processing (Monaghan et al., 2017), who observed a hemispheric asymmetry after overnight sleep for recognition accuracy in the DRM paradigm. Second, we tested the relation between sleep architecture and false memory, not only for sleep stages but also for sleep spindles.

For the first objective of the sleep false memory behavioural effects, we found that unseen-lure words were more likely to be falsely recognised after a nap,

than after a period of wake, consistent with the literature of sleep increasing false memories compared to an equivalent period of wake (Diekelmann et al., 2010; Monaghan et al., 2017; Pardilla-Delgado & Payne, 2017; Payne et al., 2009). The subsequent signal detection analyses demonstrated that the enhanced false memories were not only due to changes in response bias, but were effects of sleep on discriminability between unseen lure and unseen new words.

Studies of false memories using the DRM paradigm have used a variety of methodologies. For instance, many previous studies that demonstrated increased false memory effects after sleep have used a free recall task (Diekelmann & Born, 2010; Pardilla-Delgado & Payne, 2017; Payne et al., 2009), while those using a recognition task may find no initial effect (Diekelmann et al., 2008; Lutz et al., 2017; Pardilla-Delgado & Payne, 2017), or even reduction of false memories (Fenn et al., 2009) after an interval of sleep. In a meta-analysis of associative memory effects and sleep, Chatburn, Lushington, and Kohler (2014) noted that recall tasks are more likely to elicit false memory effects than recognition tasks, though this was concluded from only a very small set of studies. One explanation for this behavioural difference is due to the reinstatement of context that results from viewing the stimuli again in the recognition task, which can increase source-monitoring effects (Cabeza, Rao, Wagner, Mayer, & Schacter, 2001; Roediger, Balota, & Watson, 2001; Underwood, 1965) and consequently reduce false memories. Recall tasks, however, do not provide such a strong reinstatement of context for the participant (cf. Chatburn et al., 2014). Presenting stimuli visually rather than auditorially (as in Diekelmann et al., 2010; Pardilla-Delgado & Payne, 2017; Payne et al., 2009) may also decrease false memory effects again due to increased source monitoring from visual presentations (Cleary & Greene, 2002; Kellogg, 2001; Smith & Hunt, 1998; Smith et al., 2005).

However, in our study, we did find that sleep influenced false memories in a recognition memory test after a nap, but much of this effect was lateralised to the RH. Lateralising stimuli to the RH may highlight false memory effects, but naps

rather than overnight sleep may also increase false memory effects (Chatburn et al., 2014). Indeed, the results of our study, and that of previous studies of lateralisation of DRM stimuli (Bellamy & Shillcock, 2007; Ito, 2001; Monaghan et al., 2017; Westerberg & Marsolek, 2003) are consistent with the possibility that false memories may be generated in the RH. Dominance of false memory generation in the RH would be consistent with the two principal theories for sleep-induced processing changes associated with false memories – the gist theory (Brainerd & Reyna, 2005; Durrant & Lewis, 2009; Fischer et al., 2006; Gomez et al., 2006; Lutz et al., 2017; Wagner, Gais, Halder, Verieger, & Born, 2004) and the increased spreading activation theory (Cai et al., 2009; Monaghan et al., 2013). In terms of gist, precise memory for items experienced would be consolidated with the long-term vocabulary store in the LH (Tamminen et al., 2011, 2013), whereas the theme or topic of the list would be activated in the RH, enabling separation of gist and item memory in the iOtA model (Lewis & Durrant, 2011). This separation of precise and generalised semantic memory is also at the core of processing advantages for distinguishing focused and diffuse semantic associative networks across the LH and RH (Beeman, 1998; Beeman & Bowman, 2000; Monaghan et al., 2004). In terms of the spreading activation theory of sleep (Cai et al., 2009), false memories are more likely to be generated in the RH in response to increased spreading activation as unseen lure words become more highly activated in the RH, due to their interconnections to seen old words that occurred in the list. In the LH, the more localised associations between words are less likely to promote co-activation between old seen words and unseen lure words resulting in reduced false memory effects.

These two theories are by no means incompatible: Spreading activation could well underlie generation of gist from a list of related information (Howe et al., 2012). However, correlating behaviour with sleep architecture enables convergence on the mechanisms that produce the observed behavioural effects. This was the goal of our second key objective in investigating sleep stages and spindles relating to false memory effects.

We did not replicate the previous observation of a correlation between SWS duration and false memory effects in a recall task (Payne et al., 2009). Though Pardilla-Delgado and Payne (2017) found a correlation between SWS and false memory in a recognition test, they also did not replicate the correlation in a recall task. The effects, then, are somewhat variable, and this may be the reason for the absence of the effect in our study. However, we did find a strong correlation between lateralised stage 2 sleep spindles and false memory generation in our study, contributing to a growing literature on the role of spindles in memory consolidation (Diekelmann & Born, 2010; Rasch & Born, 2013; Tamminen et al., 2013). Our results showed that higher density of sleep spindles in the RH relative to the LH correlated with higher occurrence of false memories. Curiously, greater RH than LH sleep spindles correlated with both LH and RH false memories, though the latter failed to reach significance. Thus, the effects of spindles may be not only to increase false memories as a consequence of RH lateralised spindles, but also to reduce false memories as a consequence of LH lateralised spindles.

These effects were driven by stage 2 fast spindles measured at centro-parietal electrodes. These spindles have been linked to hippocampal activity, and occur in similar regions to the proposed site of lexical semantic processing in the LH (Dumay & Gaskell, 2007, 2012; Ellis et al., 2009) and RH (Beeman & Bowden, 2000). Spindle density has also been linked to consolidation of verbal material with the LH long-term vocabulary store (Tamminen et al., 2013), and van der Helm et al. (2011) observed that veridical episodic memory was positively correlated with stage 2 fast spindles, measured over the C3 (i.e., left lateralised) electrode. Thus, lateralised spindles may highlight consolidation of information with the semantic network within that hemisphere. If this is the case, then sleep spindles aid transfer of information from hippocampus to neocortex, where the structure of the long-term information in neocortex varies according to the hemisphere.

In summary, we found that whereas sleep increased overall false memory recognition, this varied according to the hemisphere that was being accessed during

retrieval, with the RH being more susceptible to unseen-lure acceptance while the LH was found to be more resilient to accepting unseen-lure words. These effects were correlated with lateralised sleep spindles to the RH compared to the LH, which indicate that sleep spindles in the RH may relate to generation of false memories whereas sleep spindles in the LH relate to reduced false memory effects.

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Highlights

A daytime nap promotes false memories of words.

Sleep enhances false memories in the right hemisphere.

Sleep spindles in the right hemisphere promote false memories.