Hemispheric processing of memory is affected by sleep

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Abstract

Sleep is known to affect learning and memory, but the extent to which it influences behavioural processing in the left and right hemispheres of the brain is as yet unknown. We tested two hypotheses about lateralised effects of sleep on recognition memory for words: whether sleep reactivated recent experiences of words promoting access to the long-term store in the left hemisphere (LH), and whether sleep enhanced spreading activation differentially in semantic networks in the hemispheres. In Experiment 1, participants viewed lists of semantically related words, then slept or stayed awake for 12 hours before being tested on seen, unseen but related, or unrelated words presented to the left or the right hemisphere. Sleep was found to promote word recognition in the LH, and to spread activation equally within semantic networks in both hemispheres. Experiment 2 ensured that the results were not due to time of day effects influencing cognitive performance.

Keywords: sleep; hemispheric lateralization; memory consolidation; false memory; spreading activation

Hemispheric Processing of Memory is Affected by Sleep

1. Introduction

There is substantial evidence that sleep affects the way in which we encode and retrieve memories (See Marshall & Born, 2007 for a review), improving both procedural and declarative memory relative to an equivalent time awake (Rasch & Born, 2013; Stickgold & Walker, 2005; Walker & Stickgold, 2006). For declarative memories, an influential theoretical model suggests that sleep promotes transference of information from recent memory storage in the hippocampus to be integrated with the neocortex (McClelland, MacNaughton, & O'Reilly, 1995). Hippocampal networks associated with spatial memory acquisition, for instance, have been observed to be reactivated during slow-wave sleep, and hippocampal activity levels during sleep are correlated with improved performance in subsequent tests (Peigneux et al., 2004).

For language processing, a growing body of work has demonstrated that sleep can enhance the reactivation of recently experienced stimuli in accordance with previously learned material, compatible with the hippocampal to neocortex transfer model of sleep (Bowers, Davis, & Hanley, 2005; Dumay & Gaskell, 2007, 2012; Lindsay & Gaskell, 2013; Tamminen, Lambon Ralph, & Lewis, 2013; Tamminen, Payne, Stickgold, Wamsley, & Gaskell, 2010). Such reactivation of words interacting with the long-term vocabulary store is likely to result in lateralisation of processing to the left hemisphere. Lateralised visual word processing tasks, where presentation to the left visual field (LVF) results in initial involvement of the right hemisphere (RH), and stimuli presented to the right visual field (RVF) project initially to the left hemisphere (LH), enable an assessment

of the extent to which stimuli are asymmetrically represented. For word naming or lexical decision tasks, a RVF/LH advantage tends to be observed (Ellis, 2004; Pirozzolo & Rayner, 1977), implying direct access to vocabulary stored in the RVF/LH. If consolidation during sleep facilitates the reactivation of declarative information within hippocampal systems (e.g., Rasch, Büchel, Gais, & Born, 2007), affecting in turn access of the long-term stored representations of words in the neocortex, then it is likely that sleep will result in a RVF/LH advantage for recognition of previously experienced word stimuli. Note that such an effect would not be due to initial encoding of stimuli in the hippocampus. Small, Nava, Perera, DeLaPaz, Mayeux, and Stern (2001) recorded hippocampal activation of participants hearing names or seeing faces. They noted no hemispheric asymmetries in hippocampal activation when encoding or retrieving these stimuli (see also Hocking, McMahon, & de Zubicaray, 2009, for similar results in a picture naming task). Similarly, there are no observed hemispheric asymmetries in hippocampal activation for visual word recognition tasks (Price, 2012). Thus, any emergence of asymmetric effects in behavioural responses could be the consequence of changes in reactivation patterns during sleep.

Whereas sleep has a beneficial effect for memory of unrelated stimuli, the effect is more nuanced for memory of words with related meanings. The Deese-Roediger-McDermott (DRM) paradigm (Roediger & McDermott, 1995) exposes participants to lists of closely related words (e.g., *bed, dream, night, drowsy, pillow*, etc). Then, participants are tested either on their recall or their recognition of words classified according to those that were in the list (old words), those that did not appear but were closely related to words in the list (lure words, e.g., for the above list, *sleep*), or those that

were unrelated to words in the lists (new words). Participants are more likely to recall, and accept as previously seen in recognition tests, lure words than new words (McDermott, 1996; Miller & Gazzaniga, 1998; Roediger & McDermott, 1995; Roediger, Watson, McDermott, & Gallo, 2001; Stadler, Roediger, & McDermott, 1999; Underwood, 1965). Payne et al. (2009) found that participants that slept between exposure to DRM lists and testing demonstrated more acceptance of lure words (termed false memories) and old words than participants who stayed awake between sessions (see also Diekelmann, Born, & Wagner, 2010; Fenn, Gallo Margoliash, Roediger, & Nusbaum, 2009; McDermott, 1996; Straube, 2012). However, it is to be noted that there are mixed results using the DRM paradigm, in terms of whether sleep increases (Darsaud et al., 2011; Diekelmann et al., 2010; McDermott, 1996; Payne et al., 2009), decreases (Fenn et al., 2009), or has no effect (Diekelmann et al., 2008) on false memory rates, which are partly due to differences between recognition versus recall tests, but also possibly due to the particular semantic properties of the DRM lists used.

One possible mechanism to account for observations of increased false memories is that sleep increases spreading activation in semantic memory (Cai, Mednick, Harrison, Kanady, & Mednick, 2009; Payne et al., 2009; Sio, Monaghan & Ormerod, 2013). This has the consequence that activation can pass from words in the related list to words which were not experienced but that are similar in meaning to those previously viewed. If sleep affects spreading activation, then we would expect to observe an increase in lure word acceptance. If this spreading activation is equal across the hemispheres then such an increase in lure word acceptance should be seen in both hemispheres. However, the properties of semantic networks in the two hemispheres are known to be distinctive. The

LH processes words with a narrow activation of other closely-related words, and the RH co-activates a broader network of associated words (Beeman, 1998; Beeman & Bowden, 2000; Burgess & Simpson, 1988; Chiarello, 2003; Kacinik & Chiarello, 2007; Monaghan, Shillcock, & McDonald, 2004), analogous to the coarse- and fine-coding asymmetries of visual processing in the two hemispheres (Brady, Campbell & Flaherty, 2005; Christman, Kitterle & Hellige, 1991; Hsiao, Cipollini, & Cottrell, 2013; Monaghan & Shillcock, 2004; Sergent, 1982).

Indeed, lateralisation studies of DRM lists, without sleep, demonstrate asymmetries in performance relating to asymmetries in LH and RH semantic processing: Lure words are generally more likely to be accepted when presented to the LVF/RH than the RVF/LH (Bellamy & Shillcock, 2007; Faust, Ben-Artzi, & Harel, 2008; Giammattei & Arndt, 2012; Ito, 2001; Westerberg & Marsolek, 2003). These results are consistent with a broader spread of activation in processing words in the RH than LH (Howe, Wimmer, Gagnon, & Plumpton, 2009; Monaghan, Ormerod, & Sio, 2014).

It is therefore possible that previous studies of the effect of sleep on DRM lists (e.g., Payne et al., 2009) in increasing the effect of lure word acceptance is actually due to an increase in the role of the RH broader semantic network in word memory tasks. There is reason to suspect that DRM sleep effects may be due to RH lateralisation, as the RH tends to be more active than the LH during the first half of a night of sleep (Bolduc, Daoust, Limoges, Braun & Godbout, 2003; Casagrande & Bertini, 2008; Casagrande, Violani, De Gennaro, Braibanti, & Bertini, 1995; Gordon, Frooman & Lavie, 1982; Natale, 2002; Natale, Lehnkering and Siegmund, 2010; Natale, Martoni, Esposito, Fabbri. & Tonetti, 2007; Violani, Casagrande, & Testa, 1998). If this explanation is

sound, then the effect of sleep on false memory would be due to the same source as the enhanced false memory effect in the RH. In this case, we would expect an interaction between LH and RH processing and sleep, rather than a general increase in lure word acceptance in LH and RH following sleep.

To summarise, there are two possible contributions of sleep to lateralisation of language processing in word memory tasks. First, if sleep facilitates reactivation of memories of words in the lists with the long-term vocabulary store, then we would observe an interaction between hemisphere and sleep or wake in terms of overall accuracy of recognition, with a shift to the LH consequent on sleep. Second, sleep may affect spreading activation in the brain's semantic associative networks. If sleep increases the role of the RH in processing, then we would expect an interaction between hemisphere and sleep or wake for lure words, with sleep particularly increasing RH lure word acceptance. Alternatively, if sleep affects spreading activation in both hemispheres equally, then we would expect to see an additive effect of sleep and hemisphere on lure word acceptance.

To test these hypotheses, we exposed participants to DRM lists, then tested their lateralised recognition of words, lure words, and unrelated words. In Experiment 1, participants either slept or stayed awake between initial exposure and testing. In Experiment 2, we tested the influence of time of day of encoding and retrieval on any observed lateralisation effects. To assess performance, we measured both accuracy and response time of recognition judgments.

2. Experiment 1: Effect of sleep or wake on hemispheric processing of memories

In this study, we presented participants with lists of words using the DRM paradigm, and then, after a 12 hour delay involving either sleep or a period of wakefulness, we tested participants' lateralised recognition memory for old words, lure words, and new unrelated words to the original lists.

2.1. Method

2.1.1. Participants

There were 62 participants with mean age 26.6 years (SD = 1.8, range 17 to 78), who were either friends or relatives of the researchers or undergraduate participants who took part for course credit. Participants gave informed consent prior to the study and were aware that they could withdraw at any time. All participants were fully debriefed at the end of the study. Sample size was based on the sleep and wake groups of Experiment 1 of Payne et al. (2009), who tested 30 participants per group. Participants were invited to participate in groups of 2 to 3, and testing was stopped after 30 or more participants had been tested.

2.1.2. Materials

Lists of DRM word stimuli were taken from Stadler et al.'s (1999) norms. Twelve lists of words were selected for the training period, corresponding with the critical lures: *car, chair, doctor, bread, fruit, sleep, thief, river, needle, music, mountain, king.* The lists corresponded to lure words that resulted in false memories in the range 30-70%. Each list

comprised 10 words, randomly selected from the 15 words provided in the original lists in Stadler et al. (1999).

For testing, 48 words were used, two previously seen from each DRM list (total of 24), one lure word for each group (total of 12), and one unseen, unrelated word for each group (total of 12). Unrelated words were taken from unused lists in Stadler et al. (1999). All words were presented in lower case Courier New bold black font in 18 point.

To test for handedness, we used the Edinburgh Handedness Questionnaire (Oldfield, 1971). We also gathered data on sleeping habits, and caffeine and alcohol intake using a short questionnaire.

2.1.3. Procedure

Participants were randomly allocated to one of two conditions, where participants were trained on the stimuli at 9am and tested at 9pm the same day (the wake group), or trained at 9pm and tested at 9am the next day (the sleep group).

At the first session, participants first completed the handedness questionnaire and the sleep habit questionnaire. Then, participants were presented with the 12 lists of 10 words. Participants sat approximately 60cm from a computer screen and were instructed to try to memorise the words that were about to appear on the screen. A fixation point appeared at the centre of the screen for 500ms. Then, the 10 words from one of the lists were presented in randomised order one word at a time in the centre of the screen for 1500ms each. After every list, participants attempted to solve a series of 3 simple maths puzzles presented for 10000ms each as a distractor task in order to prevent rehearsal of the word lists. The puzzles were randomly selected per participant, and were a different

set following each DRM list. Then, the fixation cross reappeared and the words from the next list were presented. The order of the lists was also randomised across participants. In an additional session, participants viewed a series of pictures of faces with the instruction to memorise the faces. These were not analysed in the study and are not further reported.

Participants were asked to return 12 hours later. Participants in the wake group were instructed not to have a nap, and participants in the sleep group were instructed to sleep according to their usual routine. A questionnaire was used to ensure that participants had followed these instructions.

At the second session, the test words (old, new, and lure) were presented to participants either to the left or right of centre on a computer screen. The presentation of particular words to the left or right was counterbalanced across participants, and the order of words, and lateralisation of presentation, was randomised for each participant during testing. Participants first viewed a fixation cross for 500ms, then one of the test words was presented lateralised for 120ms so as to prevent saccadic eye movement to the stimuli. Participants were required to respond with a key press as to whether the word was previously seen or not, and there was no response deadline. Half the participants responded with their left hand for previously seen and right hand for not previously seen, the other half responded with the opposite hands. Then 500ms after the response, the fixation cross reappeared for the next stimulus. Lateralised stimuli were presented with the centre of the word four characters either to the left or right of screen centre, which was approximately 2.5cm from the fixation point (2.9 degrees). Stimuli were up to 8 characters long, so all stimuli were presented to one side of the fixation point, subtending between 2.9 and 4.5 degrees.

Using the criterion applied by Diekelmann, Landolt, Lahl, Born, and Wagner (2008), we omitted participants who had less than 6 hours of sleep before the second test session, which removed 6 participants from the study. We also omitted two participants who were left handed, resulting in 28 participants in the sleep group and 26 participants in the wake group.

2.2. Results and Discussion

2.2.1. Accuracy

Analyses of the effect of response hand to previously seen or previously unseen stimuli resulted in no significant main effect or interactions with other variables, and so was not considered further in the analyses.

Table 1 shows the results for each word type distinguished by hemisphere and sleep and wake group. The data for new word responses were not normally distributed, Shapiro-Wilks test $p < .003$, however, homogeneity of variance across conditions was not significantly different, Levene's test $p > .45$. As ANOVA is robust to non-normal distributions, but not to homogeneity of variance (Glass, Peckham, & Sanders, 1972), and because transforming data is consequently not advantageous for ANOVAs (Games & Lucas, 1966), we proceeded with the parametric analysis. Though responses to old words were accurate with a yes response, and responses to lure and new words were accurate with a no response, we included all three word types in the analyses for consistency with previous studies of false memory effects with sleep, and because we hypothesised that responses to all word types would involve similar cognitive processes in terms of activation of the same semantic associative networks. We conducted a 3 way mixed

ANOVA with response accuracy as the dependent variable, word type (old, new, or lure) and hemisphere (LH, RH) as within subjects factors and sleep or wake group as a between subjects factor. There was a main effect of word type, $F(2, 104) = 86.588$, $p < .001$, $\eta_p^2 = .625$. New words (M = .782, SD = .172) were more accurately responded to than old words (M = .638, SD = .154), $p < .001$, which were more accurately responded to than lure words (M = .347, SD = .172), $p < .001$. Thus, there was an overall effect of whether new words were related or unrelated to previously seen lists, in line with previous studies using DRM lists. There was no overall main effect of hemisphere, $F < 1$, or of sleep or wake group, $F (1, 52) = 2.355$, $p = .131$, $\eta_p^2 = .043$.

<Table 1 about here>

There was a significant word type by sleep or wake group interaction, $F(2,104) = 5.329$, $p = .006$, $\eta_p^2 = .093$, see Figure 1, upper panel. Subsequent simple main effects analyses indicated that the interaction resulted from one performance difference. The lure words produced a reliable difference between the sleep and wake group, with the sleep group accepting more lures than the wake group, $F(1, 52) = 12.707$, $p < 0.001$, $\eta_p^2 = .196$. There was no significant sleep compared to wake difference for the old words, $F (1, 52) = 2.245$, $p = .140$, $\eta_p^2 = .041$, or the new words, $F < 1$. The previously observed sleep enhancement for DRM lure words was thus replicated (Payne et al., 2009; Diekelmann, Born, & Wagner, 2010).

<Figure 1 about here>

<Figure 2 about here>

Critically, there was also a significant hemisphere by sleep or wake group interaction, $F(1,52) = 4.963$, $p = .030$, $\eta_p^2 = .087$, see Figure 2, upper panel. This demonstrated that there was a statistically non-significant RH advantage for the wake group, consistent with word recognition memory studies with longer encoding to retrieval latencies (Barca et al., 2011; Federmeier & Benjamin, 2005; Oliveira, Perea, Ladera, & Gamito, 2013), which shifted to a statistically non-significant LH advantage following sleep. This behaviour was consistent with integration of recent experiences with long-term vocabulary store (Dumay & Gaskell, 2007, 2012; Tamminen et al., 2010) in the LH (Ellis, 2004). Though the overall interaction is the key aspect of these data, simple main effects analyses revealed that, for words presented to the LVF/RH, the wake group responded more accurately than the sleep group, $F(1,60) = 8.316$, $p = .005$, $\eta_p^2 = .122$, but words presented to the RVF/LH were not significantly different in accuracy of responding according to sleep or wake group, $F < 1$. The difference between LVF and RVF presentations was not significantly different for the sleep group, $F(1, 27) = 2.259$, $p = .144$, $\eta_p^2 = .077$, nor for the wake group, $F(1, 25) = 2.753$, $p = .110$, $\eta_p^2 = .099$.

There was no significant interaction between word type and hemisphere, nor was there a significant three-way interaction, both $F < 1$. These results indicate that the effect of sleep in increasing false memories was not lateralised to either hemisphere, so was thus more likely to be compatible with the hypothesis that sleep affects spreading activation across both hemispheres.

2.2.2. Response times

To ensure that the observed accuracy effects were not strategic, due to speed-accuracy trade-off effects, we also analysed response times for correct responses. Two participants' data were unavailable for response time analysis due to data-logging errors. We applied a filter removing responses that were slower than 2500ms, and faster than 150ms, resulting in omission of 5.2% of the data points. Note that this resulted in variation in the degrees of freedom because for some conditions the filtering resulted in empty cells for certain participants. We investigated other filters, but found that increasing the upper-limit reduced substantially the signal to noise ratio (e.g., SNR for 2500ms = 4.35, for 3000ms = 3.66), affecting the power of the analyses to determine an effect.

We conducted a 3 way mixed ANOVA with response time as the dependent variable, word type (old, new, or lure) and hemisphere (LH, RH) as within subjects factors and sleep or wake group as a between subjects factor. The results were largely similar to the effects of accuracy.

There was a main effect of word type, $F(2, 70) = 4.564$, $p < .001$, $\eta_p^2 = .115$. Lure words (M = 1114ms, SD = 354) were slower to be rejected than old words were accepted (M = 961ms, SD = 240), $p = .025$. Lure words were also slower than new words (M = 1020ms, SD = 241) to be rejected, $p = .027$. Old and new words did not differ from one another, $p = .996$. This pattern of response times demonstrate that the greater difficulty participants had in rejecting lure words was reflected in both accuracy and response times.

There was a significant main effect of hemisphere, $F(1, 35) = 14.166$, p = .001, $\eta_p^2 = .288$, with quicker responses to RVF/LH (M = 990ms, SD = 223) than LVF/RH (1060ms, SD = 290), again consistent with a LH advantage for word recognition (Ellis, 2004). There was no significant main effect of sleep or wake group, $F < 1$. There was no significant word type by sleep or wake group interaction, $F(2, 70) = 1.966$, $p = .148$, $\eta_p^2 = .053$, see Figure 3, upper panel. The effect of sleep on false memories in the accuracy analysis was thus not due to a speed-accuracy trade-off in participants' responses.

<Figure 3 about here>

<Figure 4 about here>

Importantly, the hemisphere by sleep or wake group interaction was significant, $F(1,35) = 5.770$, $p = .022$, $\eta_p^2 = .142$, see Figure 4, upper panel. The effect was similar to that of the accuracy analysis, with a shift from a RH to a LH advantage, in terms of shorter response times, following sleep. As with the accuracy analysis, the interaction itself is the key property of the data, but simple main effects analyses revealed that the wake and sleep groups did not differ for presentations to the LVF/RH, $F(1, 50) = 2.386$, $p = .129$, $\eta_p^2 = .046$, nor to the RVF/LH, $F < 1$. However, the difference between LVF/RH and RVF/LH presentations was significantly different for the sleep group, $F(1, 25) = 4.687$, $p = .040$, $\eta_p^2 = .158$, but not for the wake group, $F(1, 25) = 1.028$, $p = .320$, $\eta_p^2 = .039$.

Again, as for the accuracy analyses, there was no significant interaction between word type and hemisphere, nor was there a significant three-way interaction, both $F < 1$.

Taken together, the accuracy and response time analyses demonstrate that sleep enhances LH processing of words in terms of overall accuracy and response times, consistent with the view that sleep assists reactivation of recent experiences, encoded in the hippocampus, in accordance with their long-term store in the LH neocortex. In terms of spreading activation, the results are consistent with the hypothesis that sleep promotes activation in a semantic network equally in both hemispheres, but the results are not consistent with the view that sleep increases the role of the RH semantic network in word recognition tasks.

Time of day effects are known to exert an influence on cognitive task performance, with better performance generally for tasks presented in the morning compared to the evening (Schmidt, Collette, Cajochen, & Peigneux, 2007). As we were testing the effect of overnight sleep, there was an unavoidable confound in the time of day of training and testing of participants. The wake group were trained in the morning and tested in the evening, and the sleep group were trained in the evening and tested in the morning. Thus, any differences between these groups could have been due to better encoding in the morning by the wake group, or better recognition in the morning by the sleep group. In addition to diurnal effects, there are also possible lateralisation effects that are due to time of day of testing, rather than being sleep-related lateralisation processes (e.g., Natale et al., 2010). The next study tested this, using a similar methodology to previous controls of sleep effects on memory for word lists (Fenn et al., 2009; Pace-Schott & Spencer, 2012; Payne et al., 2009).

3. Experiment 2: Effect of time of day on hemispheric processing of memories

In order to measure the contribution of time of day effects to hemispheric processing performance, we tested two additional control groups, one which was trained and tested in the same session in the morning, and the other which was trained and tested in the evening. Though this design cannot perfectly control for the effect of time of day on *retention* performance, it does enable us to control for potential time of day effects on encoding and retrieval. If the qualitative differences in performance were not due to sleep but rather time of day effects, then we would expect similar interactions as in Experiment 1 but between morning and evening groups, rather than sleep and wake groups.

3.1. Method

3.1.1. Participants

There were 60 participants with mean age = 19.3 years (SD = 1.7, range 18 to 28), who were undergraduate participants taking part for course credit. Participants gave informed consent and were fully debriefed after the study. Sample size was determined to be similar to that of Experiment 1.

3.1.2. Materials

The same stimuli as used in Experiment 1 were employed in this study. Handedness was tested in the same way as Experiment 1.

3.1.3. Procedure

Participants were randomly allocated to either a morning (9am) or an evening (9pm) testing condition. Initial exposure to the words and testing of recognition memory

was conducted in a single session. First, participants completed the handedness questionnaire and then the questionnaire on their sleep habits. Then, they saw the 12 lists of 10 words in exactly the same way as in Experiment 1. After a 5-minute period of quiet rest, participants then proceeded to the test, where they saw old, new, and lure words presented either to the left or right visual field, exactly as in Experiment 1. Response hand was counterbalanced across participants.

3.2 Results and Discussion

Three participants in the morning group and two in the evening group were left-handed and so were removed from further analyses. There were no significant effects of response hand for the accuracy or response time analyses, so this was not considered in the final analyses.

3.2.1. Accuracy

Descriptive statistics are reported in Table 1. We conducted a 3 way mixed ANOVA on response accuracy, with morning or evening group as a between subjects factor, and word type (old, new, or lure) and hemisphere (LH, RH) as within subjects factors. The main effects were similar to those of Experiment 1. There was a main effect of word type, $F(2, 106) = 42.396$, $p < .001$, $\eta_p^2 = .444$. New words (M $= .757$, SD $= .225$) were more accurately responded to than old words (M $= .634$, SD $= .159$), $p < .001$, which were more accurately responded to than lure words (M $= .387$, SD $= .209$), $p < .001$, again replicating the false memory effect from the DRM stimuli. There was no significant main effect of hemisphere, $F < 1$, but the morning group responded more accurately overall than the evening group, $F(1, 53) = 5.178$, $p = .020$, $\eta_p^2 = .097$.

There was no significant word type by morning or evening group interaction, $F(2,106) = 1.792$, $p = .172$, $\eta_p^2 = .033$, see Figure 1, lower panel. However, there was a (non-significant) difference between the morning and evening groups for lure word recognition accuracy. There was no significant hemisphere by group interaction, $F < 1$, again unlike the sleep versus wake comparison in Experiment 1, as shown in Figure 2, lower panel. Thus, the greater accuracy of the RH in the wake group, tested in the evening, was not due to time of day of testing, and nor was the boost to LH processing in the sleep group driven by lateralisation of processing due to time of day effects. The interaction between hemispheres and word type and the three way interaction were also not significant, both $F < 1$.

In order to test whether the effect on lure words was greater in sleep versus wake compared to morning versus evening, we conducted an omnibus ANOVA with data collected across the two experiments. An ANOVA on lure word accuracy with sleep, wake, morning and evening as levels of the group factor resulted in a significant main effect of group, $F(3, 105) = 4.029$, $p = .009$, $\eta_p^2 = .103$, with post hoc comparisons indicating that there was a significant difference between the sleep and wake group, $p = .003$, consistent with the results presented for Experiment 1. There was also a significant difference between the sleep and morning groups, $p = .004$, but no significant differences between other groups (sleep and evening, $p = .109$; wake and morning, $p = .918$; wake and evening, $p = .157$; morning and evening, $p = .185$). Thus, sleep resulted in the largest and most reliable effect of enhancing lure words. However, the lack of difference between the sleep and evening groups suggests that encoding the stimulus lists in the

evening may have additionally contributed to the false memory effect (see also Payne et al., 2009).

3.2.2. Response times

As for Experiment 1, accurate responses which were slower than 150ms but quicker than 2500ms were included in the analyses. The time filters omitted 4.5% of the data.

We conducted a 3 way mixed ANOVA on response times to correct responses, with morning or evening group as a between subjects factor, and word type (old, new, or lure) and hemisphere (LH, RH) as within subjects factors. As for the accuracy analyses, there was a main effect of word type, $F(2, 86) = 4.061$, $p = .021$, $\eta_p^2 = .086$. Old words (M = 834ms, SD = 257) were more quickly responded to than new words (M = 892ms, SD = 306), $p = .027$, and lure words (M = 937ms, SD = 374), $p = .014$, which did not differ from one another, $p = .306$. There was no significant main effect of hemisphere, $F < 1$, and no significant main effect of group, $F(1, 43) = 2.518$, $p = .120$, $\eta_p^2 = .055$.

There was a significant word type by morning or evening group interaction, $F(2, 86) = 3.678$, $p = .029$, $\eta_p^2 = .079$, see Figure 3, lower panel. The interaction was due to the morning group responding more quickly to old words than lure words, $p = .003$ and new words, $p = .039$, with lure words and new words not differing significantly, $p = .064$, together with no significant response time differences for the evening group, all $p \geq .270$. However, note that a similar effect was not observed for the accuracy data, and that the effect of sleep versus wake on false memories resulted in a difference between lure words

and both old words and new words, and so the effect of sleep on facilitating false memories cannot be reduced to a time of day effect.

There was no significant hemisphere by group interaction, $F(1, 43) = 1.612$, $p = .211$, $\eta_p^2 = .036$, as illustrated in Figure 4, lower panel. The interaction between hemispheres and word type and the three way interaction were not significant, both $F < 1$.

For the lure words across the conditions of Experiment 1 and 2, although we expected a smaller effect of group for the lure words in response times, we conducted an omnibus ANOVA with sleep, wake, morning and evening as levels of the group factor, so as to parallel the omnibus analyses of accuracy. There was a marginally significant main effect of group, $F(3, 81) = 2.560$, $p = .061$, $\eta_p^2 = .087$, with post hoc comparisons showing that the evening group was marginally significantly quicker in responding than the wake group, $p = .060$, with no other significant differences between the groups, all $p > .16$.

4. General Discussion

Our main aim in this study was to determine the extent to which hemispheric lateralisation for memory of words was affected by sleep. Previous studies raised hypotheses about two potential mechanisms associated with sleep. First, that sleep affects consolidation by reactivating previous experiences of words allied to the long-term stored representations in the LH, and second, that sleep affects spreading activation in semantic networks, with a possible boost to the role of the RH in word recognition for all word

types. Our results enable us to decide between these alternate hypotheses about lateralisation as a consequence of sleep.

In terms of reactivation of declarative memories of words on the list with long-term store, the significant interaction between LVF/RH and RVF/LH with sleep or wake group in both accuracy and response times for all words suggested that the effect of sleep was to shift processing to the LH, where the long-term vocabulary store is proposed to be accessed most effectively (Ellis, 2004; Lavidor & Ellis, 2002). This is consistent with theoretical models of the effect of sleep in terms of consolidating recent memory traces of words in the hippocampal system with long-term knowledge in the neocortex (Darsaud et al., 2011; Diekelmann & Born, 2010), resulting in more effective reactivation of memory traces of stimuli. Intriguingly, this is further consistent with word learning studies that demonstrate a correlation between quantity of lateralised sleep spindles in the LH with the extent to which new words are acquired (Tamminen et al., 2013), even though, without sleep, activation of LH and RH hippocampus appears to be similar (e.g., Hocking et al., 2009).

The observation of the hemispheric effect on recognition accuracy due to sleep in Experiment 1 did not seem to be due to circadian effects on hemispheric processing. Natale et al. (2007, 2010) noted that there is greater activity of the non-dominant hand at the time our evening group was tested, and greater activity of the dominant hand at the time our morning group performed the task. However, this asymmetry in apparent hemispheric activity according to time of day did not result in any behavioural effects on recognition memory across the hemispheres: Experiment 2 elicited no significant differences between processing for the two hemispheres for morning versus evening

groups (though the overall effect of false memories was found). It is an intriguing question about whether such asymmetries in hemispheric activity result in different approaches to cognitive tasks, and if so, which tasks they might influence. It could be that the RH increases its role in stimulus processing in the evening compared to the morning, or alternatively, the hemispheric asymmetries in activity (e.g., Natale, 2002) may be epiphenomenal, and due to recovery of the dominant hemisphere which has undergone greater activity during the day. Alternatively, and consistent with our data, sleep-related RH activity could be the driver of transference of lexical information from the RH to the LH (e.g., Barca et al., 2011).

In terms of theories of sleep affecting spreading activation, we replicated previously observed benchmark effects of sleep on lure word acceptance: Lure words are more likely to be accepted after sleep than after a period of wakefulness (Diekelmann et al., 2010; Payne et al., 2009). However, these lure word effects of sleep were not modulated by hemispheric lateralisation in our study. Thus, previous observations of the increased acceptance of lure words in LVF/RH (e.g., Bellamy & Shillcock, 2007; Westerberg & Marsolek, 2003) was not found to result from the same source as the boost to false memories as a consequence of sleep. Yet, the previously observed hemispheric effect on lure words was not reproduced in the current study. One difference between these previous studies and our Experiment 1 was that in our study there was a substantial time delay between initial exposure and test – 12 hours, instead of the often used few minutes. However, in Experiment 2, we also failed to reproduce the lateralised hemispheric lure effect, when the time delay was just a few minutes. It is possible then that our study was underpowered with regard to finding a pure hemispheric effect of the

lures. Bellamy and Shillcock (2007) used 24 lists of words, whereas we employed only 12, and Westerberg and Marsolek (2003) used 36 lists. Note that our study was designed with sufficient power to elicit the sleep effect on recognition memory, and the key test in the current study was whether this was due to an identical source to the hemispheric effect. As we replicated the sleep effect but without the hemispheric effect, this suggests that the two effects derive from distinct sources. Thus, we found no support for the increased involvement of broader semantic activation in the RH affected by sleep underlying the false memory effect.

Our results were consistent with sleep affecting spreading activation equally across the two hemispheres of the brain: Acceptance of lure words was increased to the same degree in both the LVF/RH and the RVF/LH as a consequence of sleep. However, an alternative mechanism to spreading activation is that sleep promotes abstraction away from memory of individual items, and results in encoding of the "gist" of the word lists rather than the actual words that were presented (Payne et al., 2009). Such gist has been assumed to be lateralised to the LH (Phelps & Gazzaniga, 1992). In this case, this does not seem compatible with our results, in that this account would predict a lateralisation of acceptance of lure words in the LH compared to the RH, as well as increased accuracy for distinguishing old and new words in the LH compared to the RH. As false memories were increased to an equal extent in both the LH and the RH this seems less likely as an explanation of the effects than the spreading activation account that applies to both hemispheres.

The results in this paper provide a first step to investigate the effect of sleep on cognitive consequences of hemispheric processing. We have shown that hemispheric

asymmetries in word recognition memory are influenced by sleep, consistent with theoretical models and experimental results on consolidation of lexical information with the LH long-term vocabulary store. The extent to which sleep affects hemispheric processing of other forms of stimuli is an open question. It could be that consolidation of memories for faces, for instance, is integrated with the LVF/RH advantage for these stimuli (Pirozzolo & Rayner, 1977), which would be consistent with our interpretation of the data in the current study that sleep affects consolidation with the long-term store of information. Alternatively, it could be that the effect of sleep is to enhance processing in the LH over the RH, which would again be consistent with our results, but would show that the effects of sleep promoting LH processing would be broader than applying only to visually presented words, as was tested in our current study.

Acknowledgements

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Table 1. Accuracy and response times in ms (SD in parentheses) for each word type, by hemisphere, sleep or wake group (Experiment 1), and morning and evening group (Experiment 2).

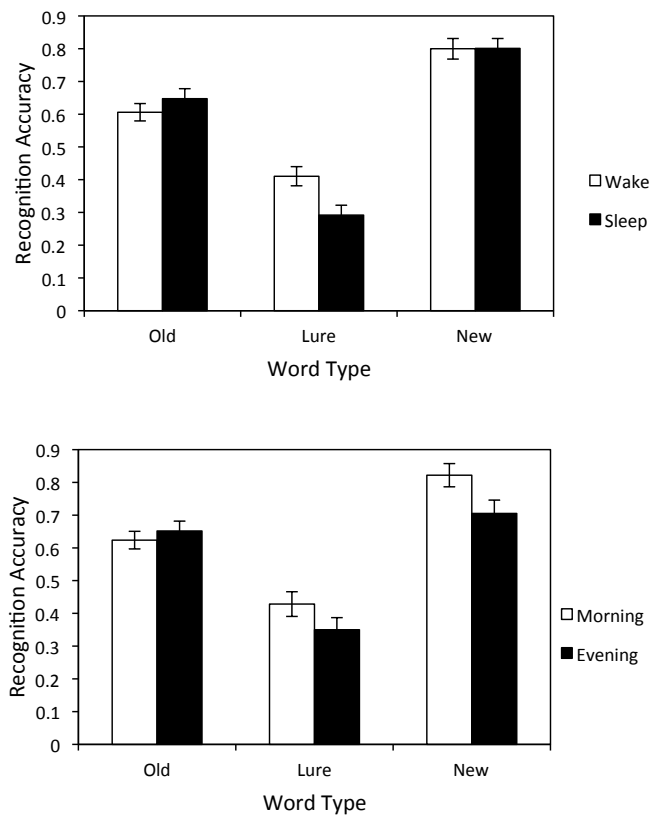|	Sleep		Wake		Morning		Evening	
	LVF	RVF	LVF	RVF	LVF	RVF	LVF	RVF
Accuracy								
Old	.65 (.22)	.69 (.17)	.62 (.22)	.59 (.16)	.62 (.18)	.63 (.19)	.64 (.18)	.66 (.18)
New	.76 (.18)	.80 (.21)	.80 (.20)	.76 (.23)	.84 (.21)	.81 (.23)	.70 (.27)	.68 (.26)
Lure	.26 (.18)	.29 (.23)	.45 (.20)	.40 (.22)	.42 (.25)	.42 (.25)	.36 (.24)	.35 (.25)
RT								
Old	1113 (347)	977 (198)	980 (283)	938 (313)	901 (280)	858 (258)	826 (325)	828 (322)
New	1206 (385)	925 (178)	984 (221)	892 (239)	989 (360)	970 (339)	837 (325)	841 (302)
Lure	1219 (419)	962 (313)	1114 (483)	1101 (331)	1079 (391)	1048 (436)	803 (345)	859 (416)

Figure 1. Accuracy of responses for each word type, for the wake and the sleep group (upper panel), and for the morning and evening groups (lower panel). Error bars show ±1 SEM.
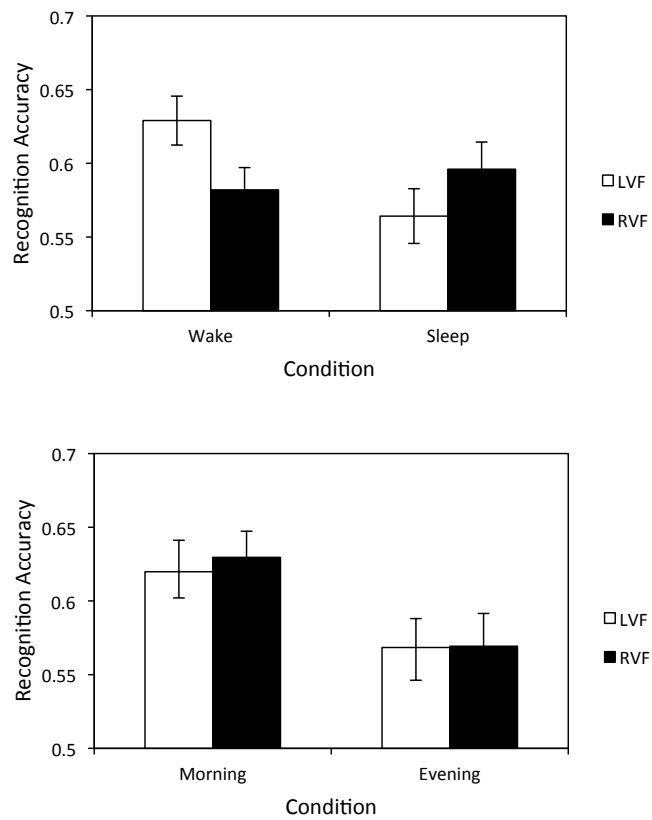
Figure 2. Accuracy of responses for words presented to the RH/LVF and LH/RVF, for the wake and sleep group (upper panel), and the morning and evening control groups (lower panel). Error bars show ±1 SEM.
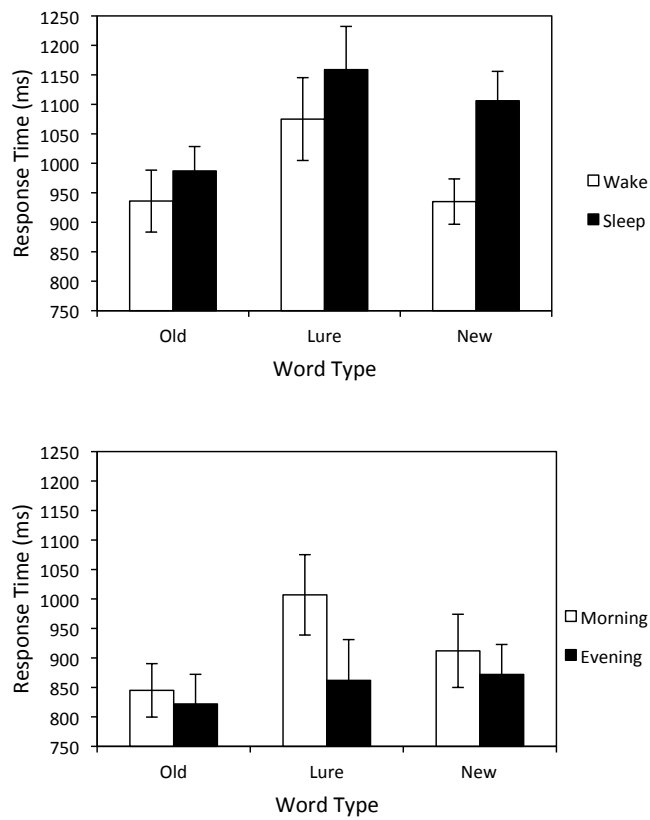
Figure 3. Response times for each word type, for the wake and the sleep group (upper panel), and for the morning and evening groups (lower panel). Error bars show ±1 SEM.
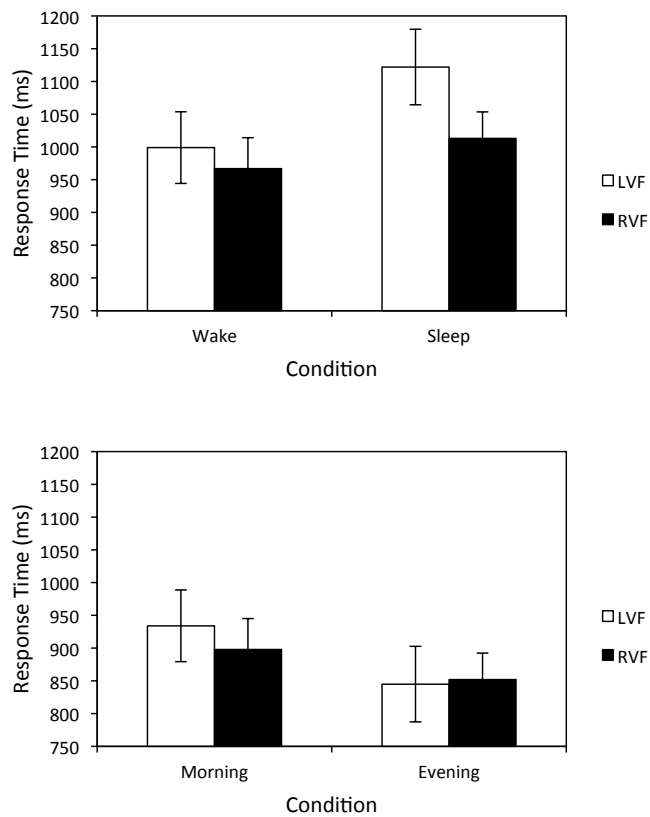
Figure 4. Response times for words presented to the RH/LVF and LH/RVF, for the wake and sleep group (upper panel), and the morning and evening control groups (lower panel). Error bars show ±1 SEM.