Hemispheric processing of memory is affected by sleep

Padraic Monaghan *, John J. Shaw, Anneliese Ashworth-Lord, Chloe R. Newbury
Lancaster University, Lancaster, UK

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, McNaughton, & 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, Lamber 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 et al. (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, Margolish, 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, Landolt, Lah, Born, & Wagner, 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 (Cal, 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 narrower activation of other closely-related words, and the RH co-activates a broader network of associated words (Beeman, 1998; Beeman & Bowden, 2000; Burgess & Simson, 1988; Chiarello, 2003; Kacinik & Chiarello, 2007; Monaghan, Shilcock, & 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 & Shilcock, 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 accurately recognised in the RH than LH (Beeman, 1998; Beeman & Bowden, 2000; Burgess & Simson, 1988; Chiarello, 2003; Kacinik & Chiarello, 2007; Monaghan, Shilcock, & 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 & Shilcock, 2004; Sergent, 1982).

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, Froeman, & Lave, 1982; Natale, 2002; Natale, Lehmkering, & Siegmund, 2010; Natale, Martoni, Elsopto, Fabbrì, & 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 h 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 17–78), 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 2–3, 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).
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