The Role of Sleep in Consolidation of Multi-Item Bound Representations

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MSc

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Prologue

This thesis has adopted the alternative format approach, thus chapters 2-5 have been written in the style of journal articles suitable for submission. Each of these chapters is independent and contains a review of the literature that is relevant to the data presented as well as a discussion relating the findings to the wider literature while Chapter 1 will provide a broader introduction to all of the work undertaken in this thesis and identify the key research questions and aims. In accordance with both department and university guidelines on alternative format thesis submission each chapter includes a full bibliography as well as a consolidated bibliography at the end of the thesis. At the beginning of each paper there is a title page containing the paper title, its submission status, followed by the pagination of the individual paper.

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Declaration

The thesis contains original work completed solely by the author under the supervision of Professor Padraic Monaghan and Dr John Towse, and has not been submitted in the same form for the award of a higher degree at this institution or elsewhere.

Name: John Shaw

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Shaw, J. J., & Monaghan, P. (2017). Lateralised sleep spindles relate to false memory generation. *Neuropsychologia*, *107*, 60–67. https://doi.org/10.1016/j.neuropsychologia.2017.11.002

Papers presented at scientific meetings

Shaw, J. J., & Monaghan, P. (January, 2017), The Impact of Sleep on the Binding of Actions, Objects and Scenes in Visual Long-Term Memory: Can repeated viewings help?, SARMAC XII, Sydney, Australia.

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Shaw, J. J., & Monaghan, P. (July 2016), The Impact of Sleep on the Binding of Actions and Scenes in Visual Long-Term Memory UK Sleep, Memory, and Language Meeting. Lancaster University, United Kingdom

Monaghan, P., Shaw, J. J., Ashworth-Lord, A., & Newbury, C. (January 2015), Lateralised False memories after a period of sleep. Royal Holloway University, United Kingdom

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It is only as I sit down to write this section that I realise how many people have helped me though this thesis. First, I have to acknowledge and thank my supervisor, Padraic Monaghan. It is hard to believe that it has now been over 4.5 years since I first came to your office on the advice of Mark Howe to discuss a possible PhD project that merged my interest of false memories with sleep. I can honestly say I could not have dreamt for a better supervisor, from your gentle nudging of me to go beyond my comfort zone to what can only be described as your scary knowledge of near enough everything, thank you for everything that has gotten me to this stage. I would also like to acknowledge and thank John Towse, my second supervisor, for all the input in various meetings and annual reviews. Next, I must thank all the various members of Padraic's lab group, of whom there are too many to name individually. Although the majority of you have no interest in sleep I always appreciated the comments and the outside perspective, it's helped shape the thesis to what it is now.

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where we can bamboozle them with sleep/false memory theory were worth the near-constant confusion!

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Dedication

In memory of John Anthony Shaw (1946-2006)

For the conversation when I was 10 that inspired me to take this path.

Abstract

A wealth of literature has demonstrated that in terms of memory representations, items are not encoded equally. In part this has been suggested to be affected by conceptual knowledge, with items with pre-existing conceptual knowledge easier to encode and thus, more salient in subsequent representations. However, it is not known how this may affect different item modalities such as actions, objects, people, and locations. As such, this thesis seeks to understand the factors that can affect the different item modalities in multi-item memory representations primarily focusing on the role of sleep, which has been demonstrated to be beneficial for memory consolidation.

In paper 1 the role of culture (Western v East Asian) was examined in differences in bound memory representations, focusing on object-scene and action-scene pairings. It was observed that culture was not a factor for action-scene pairings but Western participants were significantly more accurate than East Asian participants for object-scene pairings. Furthermore, object-scene recognition was significantly more accurate than action-scene recognition across both cultures, suggesting a difference between actions and objects in ease of recognition.

In paper 2 this was expanded to see the role of sleep in consolidation of action-scene/object-scene pairings. As with paper 1 object-scene pairings were significantly more accurate than action-scene pairings in immediate testing, and object-scene recognition experienced a benefit of sleep, with accuracy higher in the sleep group than the wake group. This difference was not replicated in the action-scene task.

Paper 3 sought to apply the previous results to a practical situation, that of eyewitness testimony as the existing literature has revealed that within eyewitness testimony participants are susceptible to errors of binding at retrieval. Across the two sessions we observed a significant difference in item modality, with action details recalled to a higher level than object, location, and people details but there was no effect of sleep/wake.

Paper 4 moved away from visual memory and instead focused on the role of sleep on conceptual knowledge using the DRM paradigm. Participants were trained on 12 DRM wordlists and then were assigned either to a short-term wake group or a nap group monitored with polysomnography. At retrieval, sleep significantly increased lure-unseen acceptance compared to the equivalent period of wake, providing evidence of sleep promoting false memory generation. Furthermore, RH spindle generation relative to LH spindle generation was significantly correlated with false recognition of lure-unseen words, suggesting a central role of the RH in false memory generation.

Chapter 1. Introduction

Chapter Summary

This chapter provides a review on the background literature that will be explored in the thesis. Within the literature three key concepts will be approached. First, the role of the hippocampus in consolidation of memory and the theoretical perspectives within the current literature. Second, the theoretical perspectives behind why memory distortions can occur, and third, the role of sleep in memory consolidation. Finally, this chapter will provide an overview of the studies to be featured in the thesis.

CH1. Literature Review

1.1 Overview

Imagine you are at Blackpool beach. You look out over the sea. The water has a murky-green colour as it mixes with the sand. Dark clouds are rolling in bringing rain. You notice a few seagulls and the differences between them. One has different colouring, is much smaller while the others are pristine white despite the water. One seagull suddenly swoops down and attacks a fish but stops once realising it is just a shoe. In our everyday life we see incredibly complex visual scenes with hundreds of details to encode ranging from the item-specific details (colour, size) to the whole image. Even more, there are several item modalities to process: the objects in the scene, the location, the actions performed, and the people present. There is a growing body of evidence for our understanding of how we can process these, with pre-existing conceptual knowledge playing an important role and in a separate strand of research that item modalities are not equally consolidated either in quantity or fidelity of the representation. Recent literature suggests a role of the hippocampus in this form of processing (Horner & Doeller, 2017), yet one area of the literature that is relatively unexplored is the role of sleep in consolidation of these bound representations. Within the literature there is much evidence of the beneficial effect of sleep on consolidation of information including both declarative and procedural (see Diekelmann & Born, 2010; Rasch & Born, 2013). More specifically, during sleep it is suggested that memories are reorganised from high-fidelity, highly-contextualised hippocampal-based episodic representations to a more conceptual, decontextualised neocortical-based representation. Moreover, having pre-existing conceptual knowledge has been demonstrated to expedite this consolidation process (van Keresten et al., 2010a, 2010b, 2013a, 2013b, 2014). There is an issue though, how may this shift in representation from contextualised to decontextualised affect the episodic representation, and can conceptual knowledge influence this? The purpose of this thesis is to explore the role of sleep in the consolidation of bound representations of differing item modalities and what factors may affect this. In the following section I will first address the various literature regarding consolidation theories then link that to research literature emphasising an important role of both conceptual knowledge and hippocampal activity. After that I will discuss the role of sleep in consolidation and highlight where there is a gap in the literature that this thesis sets out to fill.

1.2 Consolidation

1.2.1 Origins of Consolidation Theory

The topic of memory consolidation is amongst the oldest within psychology with early studies on consolidating dating back to the late 1800s. By consolidation I refer to the established concept that after learning memory representations can be strengthened after they have been formed. In pioneering research, Ribot (1882) observed a number of patients reporting retrograde amnesia following a brain injury whereby they could recall information from their childhood but events temporally close to the event were unknown. From this Ribot proposed a temporal process of memory where memories become fixed as time progresses and gradually become resistant to post-event trauma (Polster, Nadel, & Schacter, 1991). The field was expanded upon by Müller and Pilzecker (1900) who built upon Ribot's theory and applied it to healthy adults (for a summary, see Lechner, Squire, and Byrne, 1999). Within their monograph, Müller and Pilzecker reported 40 experimental conditions, focusing on participants learning lists of non-word pairs within a fixed period of time with cue-based associative memory tested after a short delay. It was observed that recall of the non-word pairs was impeded when participants immediately learnt a second list after the target list compared to an equivalent period of non-learning delay. Furthermore, if the gap was over 6 minutes between word lists, participants' recall suffered no impairment on either list, leaving Müller and Pilzecker to suggest consolidation occurred after initial encoding, and any extra material presented before consolidation could be complete can act as interference to this consolidation, reducing subsequent recall. While the literature expanded in the early 20th century with studies seeking to replicate Müller and Pilzeckers' (1900) results, it was fraught with issues. Buxton's (1943) review highlighted a lack of standardisation across the field with many studies failing to account for confounds associated with repeated testing or type of stimuli used. As such, within cognitive psychology interest in consolidation gradually declined with contemporary theories of memory assuming an unimportance of consolidation processes (see Brown & Lewandowsky, 2010 for a full review), instead preferring concepts such as interference or decay (Wixted, 2004, 2005) to account for difference in memory retention over time.

Yet within cognitive neuroscience consolidation is broadly accepted as a key process in memory. In a seminal paper, Hebb (1949) suggested a biological mechanism for consolidation of memory, proposing the dual-trace mechanism of memory that acknowledged the dichotomy between short term and long term memory. Within the Hebbian theory consolidation relied upon repeated activation of cells after stimuli offset thus allowing neuronal associative connections to strengthen in the absence of presented stimuli, neatly summarised as 'neurons that fire together, wire together', marking a shift in the literature towards an associative based consolidation model that had previously been suggested (James, 1890, Bartlett, 1932). Furthermore, Hebb's studies marked a shift in approach to consolidation from cognitive observation to biological events underlying consolidation. From this two types of memory consolidation were considered; cellular consolidation focusing on stabilisation of changes in synaptic efficiency via long-term potentiation and long-term depression occurring within hours of encoding (Frankland & Bontempi, 2005), and systems level consolidation whereby memories can be subject to change after the initial cellular consolidation. One such theory that adopted the ideas proposed by Hebb was the work of Marr (1970, 1971) who proposed a model of neuronal consolidation that occurred over several days. Marr suggested memories are initially stored in a simple memory store that is unable to be related to existing memories and in order to overcome this, these simple memory representations are transferred from the simple memory store (that Marr suggested to be within the archicortex), to the neocortex. Of particular relevance to the thesis, Marr emphasised this transfer occurs mostly during sleep.

1.2.2 Contemporary theories of Consolidation

The work of Hebb (1949) and Marr (1970, 1971) has since been used as the foundation for modern consolidation theories, resulting in theories containing a strong biological and cognitive framework. Within the literature supporting consolidation they can be split into three key models, The Complementary Learning Systems model (CLS; McClelland et al., 1995; Squire, 1992), the Multiple Trace Theory (MMT; Nadel, Samsonovich, Ryan, & Moscovitch, 2000), and the Transformation Model of Consolidation (TMC; Winocur et al., 2010). While each model may differ in specific processes, there is a consensus across all models regarding two key aspects. 1) that memory can be split into two forms of representation- episodic and semantic/conceptual (hereafter termed conceptual representation), 2) that the hippocampus and the neocortex are integral to these representations. In the following sections I will first describe and review each model of consolidation, highlighting the strengths and weaknesses in contrast to the other models and then discuss the different representations.

1.2.2.1 Complementary Learning Systems Theory

Building upon the word of Hebb (1949) and Marr (1970, 1971), the Complementary Learning Systems model of consolidation is perhaps the most widely known and researched amongst the literature (Squire, 1992; McClelland et al., 1995). Within the CLS model the hippocampus encodes sparse, non-overlapping, contextualised representations that are resilient to subsequent interference (*episodic*) while the neocortex is a more flexible system, featuring highly-overlapping, decontextualised representations that are susceptible to change over a period of time (*conceptual*), and through an interleaving of experiences, avoids the issue of catastrophic interference at reactivation: neocortical representations are long lasting while hippocampal representations are temporary. Within the model the neocortical representations are often initially represented quite poorly, with only weak connections existing between representations (Murre, 1996; Meeter & Murre, 2004a, 2004b), suggested to be in geographically disparate areas (Alvarez & Squire, 1994), and are relatively “slow”. This key characteristic of it being the slow learning system is suggested to be essential to long term consolidation, with McClelland et al. (1995) emphasising the importance of this store as essential to ensure that prior knowledge is not overwritten by incoming information thus impairing subsequent retrieval, a phenomenon termed catastrophic interference and previously demonstrated in artificial intelligence (Ratcliff, 1990). As such, within the CLS model consolidation occurs as repeated hippocampal reactivation reinstates the disparate neocortical associations further strengthening them until the point where the episodic memory within the neocortical representation is a replication of the original hippocampal representation and as such, the latter is no longer required and gradually decays (Figure 1.1).

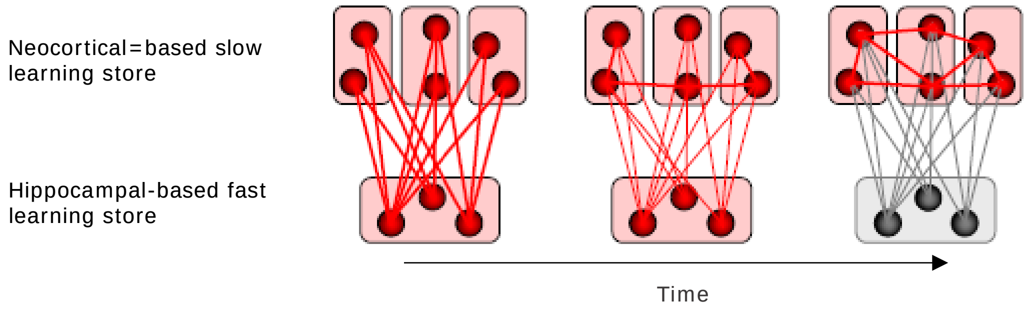

Figure 1.1. Standard model of Complementary Learning Systems. The model assumes two distinct memory systems, a hippocampal-based fast learning store and a neocortical-based slow learning stores, with both occurring in parallel. Over time through repeated activation the hippocampal store seeks to strengthen the neocortical connections until the hippocampal representation is no longer required. Figure adapted from Frankland & Bontempi (2005).

Within the literature there is substantial support for the CLS model, with evidence in both human and animal studies. Within human studies the model is demonstrated mainly in studies on amnesic patients with hippocampal or parahippocampal lesions, primarily through hypoxic patients (loss of oxygen resulting in neuronal damage), of which the hippocampus is particularly vulnerable. In one of the most famous studies in the literature Scoville and Milner (1957) reported patient HM suffered retrograde amnesia following removal of parts of his hippocampal system in order to manage epilepsy. More recently, Yonelinas et al. (2002) examined recall (*hippocampus based)* and recognition deficits in 56 participants who suffered mild hypoxia that was primarily limited to the hippocampal region. In an initial test of recall compared against recognition hypoxic participants overall demonstrated significant retrieval impairment of studied material compared to aged matched control groups, suggesting a deficit an overall deficit in retrieval. Furthermore, recall, which relies upon the ability to acquire and process memory within the hippocampus, exhibited significantly greater deficits compared to recognition, which could rely upon perirhinal based familiarity judgement. Moreover, covariation between recall, recognition, and severity of hypoxic event was examined using a structural equation model and revealed that hypoxic severity, thus hippocampal damage, predicted the degree in which recollection, but not familiarity, was impaired. Similarly, Aggleton et al. (2005) reported a similar pattern in participants who suffered hippocampal atrophy due to complications of meningitis. In patients where the damage is restricted to the neocortex, a reversal is observed: patients tend to exhibit a degradation of conceptual knowledge while episodic memories remain intact (Graham, Becker, & Hodges, 1997; Snowden, Griffiths, & Neary, 1996). In a healthy population, Takashima et al. (2009) utilised fMRI to observe hippocampal and neocortical activity in a spatial location task at immediate recall and after a delay of 24h. Comparing the two timeframes, immediate recall demonstrated greater hippocampal activity than neocortical but this imbalance reversed at 24h, with hippocampal-neocortical connectivity also decreasing by the second testing, supporting the suggestion that hippocampal representations are not as essential over time.

1.2.2.2 Consolidation Through Reorganisation

However, there is a growing body of evidence that contradicts key points of the CLS model. Since patient HM several studies have observed no temporally graded retrograde amnesia, suggesting no memory impairment, or a complete memory impairment, in some cases lasting decades (Bayley et al., 2006; Manns et al., 2003; Nadel, Winocur, Ryan, & Moscovitch, 2007), a result not compatible with CLS. As such, alternative models of consolidation have since been promoted. Nadel et al.'s (2000) Multiple Trace Theory (MMT) suggests differing roles for the two systems similar to the standard consolidation theories (SCT), memories are initially encoded in both the hippocampal and neocortical, with the neocortical representation considered to be highly-semantic and context-independent while the hippocampal representation is suggested to be a high-fidelity, contextualised representation of an episodic memory. Repeated reactivation of the hippocampal representation leads to multiple distinct traces created for the episodic memory, ensuring a long-lasting representation while also promoting common information for integration within the neocortical semantic network. Once the semantic representation is strong enough, these decontextualised memory traces no longer require hippocampal activation to be retrieved but the specific episodic memory still required the hippocampal-cortical connection.

Evidence for the MMT can be seen in studies of the dissociation between episodic and semantic memory. For example, there are reports of amnesic patients that show temporally ungraded impairment for episodic memory (Rosenbaum et al., 2001; Steinvorth et al., 2005). In a case study by Warrington and McCarthy (1988) a patient with severe retrograde amnesia was able to retain words that had occurred after hippocampal damage, e.g., ‘shuttle’ and ‘thatcherism’, demonstrating that retrograde amnesia did not impair semantic memory, suggesting a dissociation between the episodic and semantic memory. Using fMRI, Davachi, Mitchell, and Wagner (2003) observed hippocampal and perirhinal activity in participants at both encoding and retrieval within an item recognition task and observed that encoding activation in the hippocampus and posterior parahippocampal cortex predicted later item recognition.

More recently, in an effort to unify CLS and MMT a review by Winocur et al. (2010) summarised the literature by proposing the Transformation Model of Consolidation, encompassing key themes of both CLS and MMT. The key aspect of the transformation model is that the neocortical representation is significantly different to that of the hippocampus by virtue of their complementary nature. The hippocampus encodes a high-fidelity, contextualised episodic memory whereas the neocortex encodes a conceptual, decontextualised *schematic* memory and it is through repeated reactivation that the schema is modified and formed. The schematic structure allows key commonalities between memories to be consolidated in the long-term memory, allowing retrieval of the schematic representation when relevant information is experienced. Furthermore, Winocur et al. emphasise that the hippocampal representation is not as transient as CLS models would suggest, instead the original episodic memory remains in the hippocampus for as long as it can be retained. In doing so the model is able to account for the variation in retrograde amnesia observed in the literature.

1.2.3 Conclusion

To summarise, across all theories there is a consensus that there are two forms of memory representations: hippocampal-based an episodic representation that is typically contextual and stored in high fidelity form, and a neocortical semantic or *conceptual* representation that is typically context-free, but more generalisable to different scenarios (McClelland et al., 1995; Nadel et al., 2000; Winocur et al., 2010). However, they primarily differ in how they view the interaction between these representations. The CLS model adopts a relatively unidirectional view that the hippocampal episodic representation serves to consolidate the neocortical conceptual representation and once this has occurred, is free to degrade as the remote memory is available within the neocortical store. In contrast, MMT and TMC (Nadel et al., 2000; Winocur et al., 2010) adopt a view of greater hippocampal involvement in long-term memory, with the hippocampal-episodic representation serving to influence the conceptual representation but is essential for providing contextual, spatial, and temporal detail that is lost in the decontextualised, conceptual representation. Moreover, there is a growing literature suggesting that conceptual representations are also important for encoding of episodic representations. In the following sections I will first describe the literature surrounding conceptual representations, including what they are and how they are formed, before linking them to episodic memory retrieval.

1.3 Representations in Memory

Early models of conceptual representations suggested that they were stored in separate modality-specific representations of motor, sensory, and verbal information, and that conceptual knowledge represented a form of network between these modality-specific representations within a distributed neocortical network (Eggert, 1977; Martin, 2007; Patterson et al., 2007). However, subsequent evidence of semantic dementia appears to dispute this distributed view as damage to the temporal lobe results in a breakdown of conceptual knowledge across all domains, providing contradictory evidence of a distributed model of representations (Bozeat et al., 2000; Lambon Ralph et al., 1999, 2001; Piwnica-Worms et al., 2010).

The study of such patients has instead led to the prominence of a ‘hub-and-spoke’ model of conceptual knowledge, whereby concepts act as a central node to which the sensory, motor, and verbal representations can be linked (Lambon Ralph et al., 2010; Lambon Ralph, 2014; Patterson et al., 2007; Rogers et al., 2004), with the spokes forming associations through the hub. The purpose of the hub is thought to act in three key ways: integration of information across different modalities and experiences; encoding the structure of conceptual relationships via identification of commonalities across items in order to generalise to novel items; and to encode items in a way in order to allow high-order generalisation in order to allow generalisation across items that may not necessarily have the same surface-level features (e.g., knowing that a dolphin is a mammal despite all visual features indicating it may be a fish) (Rogers et al., 2004; Lambon Ralph et al., 2010; Lambon Ralph, 2014). Evidence supporting a transmodal hub model was recently demonstrated in a computational model by McClelland and Rogers (McClelland & Rogers, 2003; Rogers et al., 2004; Rogers & McClelland, 2004). Within their model modality-specific regions require additional support from a central representational unit (the hub) in order to allow cross-modal mappings and encoding of conceptual relationships. Studies on patients with semantic dementia suggest the hub is located within the anterior temporal lobe (ATL), with atrophy of the ATL linked to specific breakdown of conceptual knowledge (Brambati et al., 2009; Hodges et al., 1992; Mion et al., 2010), with a positive correlation observed between the degree of damage to the ATL and the severity of semantic impairment (Mummery et al., 2000; Nestor et al., 2006). This, combined with its close proximity to the medial temporal lobe (MTL), limbic system, and frontal cortex allow a high level of interconnectivity across important regions (Patterson et al., 2007).

1.3.1 Formation of Conceptual Representations

But how are conceptual representations formed? much of the evidence for conceptual representations suggest a form of long-term learning of elements through repeated exposure or reactivation of hippocampal based episodic representations. For example, within the previously mentioned CLS model (McClelland et al., 1995) consolidation is initially a two-stage process, encoding a fast-learning episodic representation in the hippocampus and a slow-learning conceptual representation in the neocortex. Through repeated hippocampal activation of the episodic representation, the commonalities across experiences and exemplars are extracted and form a conceptual representation independent of the episodic representation, a process referred to as semanticisation (Battaglia et al., 2011; Cermak, 1984; McClelland et al., 1995; Moscovitch et al., 2005; Meeter & Murre, 2004; Rosenbaum et al., 2001; Stickgold, 2009; Sweegers & Talamini, 2014; Westmacott et al., 2004).Within the literature there appears to be two distinct forms of conceptual formation, that of explicit, verbalised rule based learning and implicit, complex, non-verbal learning (Ashby et al., 1998; Knowlton & Squire, 1993; Nosofsky & Johansen, 2000). For the former, there are numerous studies that demonstrate the use of simple, verbalised rule based learning in various classification tasks whereby participants are able to explicitly define the categorisation rule (Ashby & Spiering, 2004; Ashby & Maddox, 2005). In complex learning, one suggestion for conceptual formation is that of similarity based-models (Ashby & Waldron, 1999). In similarity based models, categorisation of items is decided based upon similarity to existing conceptual representations (Ashby & Maddox, 2005; Medin & Rips, 2005; Palmeri & Flanery, 1999; Posner & Keele, 1968; Reed, 1972; Smith, 2001; Smith & Minda, 2002; Tunney & Fernie, 2012). An extension of this theory is that of an exemplar-based model of semanticisation (otherwise termed episodic models; Smith et al., 1998; Tunney & Fernie, 2012). Within this theory conceptual representations are formed through a composition of previously encountered category exemplars and activation of episodic representations allows subsequent categorisation of a novel item.

1.3.2 Role of Conceptual Representations in Supporting Episodic Memory

However, these theories somewhat underplay the role of the conceptual knowledge in hippocampal-based episodic memory representation. For example, although the CLS, MMT, and TMC models suggest interaction between neocortical and hippocampal representations, much of this is theorised to be unidirectional whereby the hippocampal-episodic representation forms the basis of the neocortical-conceptual representation, with little detail given to the role of conceptual knowledge in the hippocampus. This appears somewhat at odds with neurobiological literature, with neurobiological models of episodic memory such as the Hierarchical Relational Binding Theory (hRBT) of Shimamura (2010) demonstrating that the hippocampus is key to forming associations between multiple memory representations, acting as a “convergence zone” whereby disparate inputs from the MTL and neocortex are fed and bound into a single representation (Damasio, 1989; Marr, 1971; McClelland et al., 1995) that ultimately supports episodic memory, requiring both episodic and conceptual knowledge in order to create an episodic representation (Tulving, 1983). More specifically, within the hippocampus specific *concept cells* have been observed in relation to conceptual knowledge, such as animals, buildings, and celebrities (Quiroga, Reddy, Kreiman, Koch, & Fried, 2005; Kreiman, Koch, & Fried, 2000). For example, it was observed that firing of concept cells is not linked to a particular trigger, but rather their firing pattern could be activated through multiple associated stimuli, such as a written form of a celebrity’s name or a photo (Quiroga et al., 2005). Moreover, concept cells can tune their firing field rapidly, with rodent studies demonstrating that place cells can tune after a single visit to the target location (Monaco, Rao, Roth, & Knierim, 2014), and concept cells can respond to a person within hours of meeting them (Quiroga, Kraskov, Koch, & Fried, 2009). Based upon this Quiroga (2012) has suggested that these place and concept cells form the ‘building blocks’ of hippocampal bound representations acting as a form of early precursor of conceptual knowledge, allowing rapid encoding and formation of high-fidelity hippocampal representations across multiple items, creating bound representations quickly.

This rapid formation of bound representations can be beneficial in applying conceptual knowledge to new scenarios. A range of evidence from human, rodent, and computational modelling studies suggest that pre-existing conceptual knowledge can be advantageous to consolidation of novel but related material. Within rodents, Tse et al. (2007) trained rats within a location on a schematic food layout, allowing learning of the typical locations via smell. Rats were given hippocampal or control lesions at different points in training with neocortical retrieval measured by digging at previously learned food sites. While the rats lesioned 3h after learning could not generalise to novel-but-consistent reward probes, rats lesioned after 48h were able to generalise to schema consistent novelty, suggesting a time-dependent measure in consolidation of newly learned information. Furthermore, when reward probes were delivered in a schema-inconsistent manner, both task improvement and generalisation was impaired for both sets of rats. The study demonstrated that information that is compatible with pre-existing schemas can aid consolidation, even when hippocampal lesions were implemented after learning of the initial schema. Within humans, van Kesteren et al. (2010, 2013, 2014) observed through fMRI studies that prior knowledge modulated the contribution of the neocortex and hippocampus to encoding of new information.

But for the purpose of the thesis I wish to focus the beneficial effect of conceptual knowledge on visual long-term memory (VLTM). At an item level it has been demonstrated that conceptual knowledge of visual elements can affect subsequent retrieval (Esyenck, 1979; Nairne, 2006; Rawson & Van Overschelde, 2008; Schmidt, 1985; von Restorff, 1933). In a series of experiments Koutstaal et al. (2003) observed that recognition of real-world objects was better than memory for highly-distinct but novel items, suggesting that even with explicit labelling of ambiguous shapes, there is a substantial benefit of pre-existing conceptual knowledge in recognition of shapes. Furthermore, there is recent evidence that even within VLTM, the level of detail in the conceptual representation can affect the extent to which it can cue the correct representation without competing cues. In a series of studies Konkle, Brady, Alvarez, and Oliva

(2010a, 2010b) sought to compare the role of categories for various visual items in VLTM. Extending the previous literature that demonstrates that humans can have a large a detailed storage capacity to the extent of maintaining thousands of high-fidelity representations (Standing, 1973; Brady, Konkle, Alvarez, & Oliva, 2008; Hollingworth, 2004; Vogt & Magnussen, 2007), Konkle et al. examined the role of categorical and perceptual features supported long-term memory representations. Within their first study (2010a) participants viewed 2800 objects with a varying number of exemplars from each category and in a subsequent two alternative forced-choice task (2AFC) participants were presented with one of the previously seen exemplars and a second, unseen exemplar from the same category. Accuracy was consistently high across all exemplar levels, even with 16 presented exemplars (82%) but memory performance decreased as more exemplars were displayed, suggesting that while VLTM is capable of storing a large number of category exemplars, it is prone to interference when multiple items are required to be encoded. Furthermore, variations in categorical distinctiveness (e.g., a category of car could vary from a mini through to a limousine) were also found to reduce interference suggesting that while the conceptual representation can support recognition of an item, key contextual details of the item are important for specific recognition (e.g., although a limo is a car, knowing the key detail of it being longer than the average car). In a follow up study Konkle et al. (2010b) demonstrated a similar recognition rate for scene memory. Once again participants were presented with over 2900 images of scenery from 128 categories with 1, 4, 16, or 64 exemplars displayed per category. In a subsequent 2AFC task recognition rate was still consistently high, with the novel condition reporting 96% recognition accuracy against a novel item from an unseen category, dropping to 76% accuracy in the 64-exemplar category, comparable to the results of the object recognition task (Konkle et al., 2010a).

From this study Konkle et al. (2010b) suggested that it is not feasible for humans to be able to store high-fidelity representations of each individual item and as such, items within the VLTM must be represented at a conceptual level through an item prototype, a form mental representation of an item that can be linked to multiple exemplars in order to reduce cognitive load and aid consolidation of an episodic representation through accelerated consolidation of key features to be used for subsequent recognition. For example, when presented with a limousine the item prototype can automatically encode the key features of a car (four wheels, general shape) while key details can be formed in the episodic representation (in the example of a limo, the extended length of the car). In a subsequent recognition task, if participants are presented with the limo and another car, the prototype of a car can feature multiple exemplars ranging from standard hatchbacks, SUVs, cabriolets, even motorised wheelchairs, but are all able to be identified as a car but the specific episodic/contextual details of it being a limo can aid consolidation. The result is akin to examples form the verbal domain whereby familiar letter strings (e.g., FBI-BBC-NHS-MAN-UTD) are more likely to be retrieved than unfamiliar letter strings (FBIB-BCBH-SMA-NUTD; Bower & Springston, 1970) and is consistent with the previously reported research on expedited consolidation of information consistent with pre-existing conceptual knowledge (van Kesteren et al., 2010, 2013, 2014), suggesting that within VLTM, having pre-existing knowledge is beneficial. Issues of recognition or retrieval errors occur when items linked to the prototype have little variation, (e.g., compared to the previous car example, if the prototype is of a potato, in a recognition task it may be harder to distinguish a King Edward potato from a Maris Piper), or in situations whereby there is a lack of conceptual knowledge for that specific item. In that scenario, it may be that conceptual knowledge is required to create what is its best prediction of the answer in accordance with its own framework.

1.3.3 Consolidation of Bound Representations

As of yet all the discussed studies have primarily focused on a single-item presentation and how episodic and conceptual representations may form from there, but real life is rarely so singular, visual scenes are incredibly complex and include a variety of different items. For example in the image below (Figure 1.2), although the primary focus is the dog, there are multiple different items of varying complexity, including the dog (breed, colour, spatial orientation, size), the pipe (colour, size, style), and the table (colour, shape, size). As such in order to create an episodic memory of those specific elements, consolidation of all the items and associations between these must be formed early in encoding.

Figure 1.2. A dog smoking a pipe. Taken from stimuli from Standing (1973).

Within the literature the hippocampus is thought to support creation and consolidation of these episodic representations by acting as a form of ‘convergence zone' through three key mechanisms: 1) rapid learning of associations, 2) pattern separation, 3) pattern completion.

Rapid learning of new associations

As it is incredibly unlikely that you will often experience the exact same scenario multiple times, one of the functions of the hippocampus is suggested to be rapid learning of new associations that are already encoded as conceptual knowledge. Several theories posit that the hippocampus is central in this form of rapid learned association through its position within the MTL, acting as a "hub" for separate elements. Recent studies utilising fMRI support the concept of bound representations being represented in the hippocampus yet these mostly focused on the hippocampus in isolation, neglecting the wider neocortical network. One study that built upon these findings was that of Backus et al. (2016) who examined hippocampal activity using an associative memory task then measuring hippocampal activity through multivariate pattern analyses of fMRI data. Backus and colleagues observed overlapping coding within the hippocampus alongside a hub-like network, supporting the idea that information from various neocortical sites feed into the hippocampus and that this is crucial for bound representation formation.

Pattern Separation

The second proposed function of the hippocampus in supporting episodic recollection is that of pattern separation. This concept refers to the ability of the hippocampus to produce non-overlapping representations from overlapping input, acting to decrease interference between items by minimising overlap at encoding. As with much of the literature on hippocampal activity, it is primarily fMRI studies that have demonstrated pattern separation within the hippocampus, with Bakker and colleagues the first to demonstrate pattern separation within the hippocampus. Within their study participants were presented with multiple exemplars of items (e.g., two similar rubber ducks) and noted that measures of hippocampal activity decreased over repeated presentation of the stimuli (Bakker, Kirwan, Miller, & Stark, 2008), which Bakker and colleagues inferred to be the presence of pattern separation.

The effect of pattern separation can also extend to complex events with overlapping content. In a study using video stimuli Chadwick, Hassabis, and Maguire (2011) presented participants with multiple videos that combined two background and two foreground stimuli in unique pairings (e.g., stimuli a, b, c, d, could be combined as ac, ad, bc, bd). Using fMRI Chadwick and colleagues observed that the hippocampal representations could be distinguished within each video, suggesting that even in input that is highly overlapping the hippocampus is capable of producing high-fidelity, separated representations.

Pattern Completion

Furthermore, the hippocampus is capable of producing holistic recollections of episodic memory. Horner and Colleagues (2015) had participants learn complex hypothetical events consisting of multiple overlapping pairs of elements (people-location-object) within distinct neocortical regions and at retrieval episodic memory representations were targeted through a partial cue of one element (e.g., location) to retrieve a second (e.g., person), with participants monitored using fMRI at both encoding and retrieval. It was observed that participants' degree of reinstatement strongly correlated with their hippocampal activity, suggesting that episodic elements, even those in distinct neocortical regions, are bound into holistic event representations that can aid episodic recollection. Furthermore, cueing with the location of the complex event led to reinstatement of just the category (e.g., people v location) but not the exemplar-level item, suggesting that cues based upon location are useful for reinstatement of categorical elements but they are unsuitable to store high-fidelity exemplars. In situations whereby specific detail is required for information that may only vary slightly from others within a category (e.g., visual differences between species of banana), then it may be that conceptual knowledge of the overall category may be preferentially retrieved, reducing fidelity.

1.3.4 Maladaptive Influence of Conceptual Knowledge in Consolidation

However, although prior conceptual knowledge can be of great benefit for expedited encoding and consolation of schema-consistent information, this same strength can also be maladaptive in situations whereby the information is inconsistent with our prior knowledge. Early work by Bartlett (1932) demonstrated an early representation of a conceptual consolidation within the *"War of the Ghosts"*. Within the study participants read an unfamiliar story that contained culturally unfamiliar narratives set within Native American folklore but contained information not consistent with the setting. Over time participants began to make errors of commission in which they inserted unrelated information into the narrative as well as errors of omission, failing to produce information that was inconsistent with the theme, with false memories an error of commission. Importantly, Bartlett noted how the information provided by participants over time gradually changed to be more consistent with pre-existing views on Native American Folklore, with errors of omission reducing inconsistent information, and errors of commission introducing consistent. Bartlett's study was among the first in the literature to demonstrate that consolidated memory is not a direct representation of what was experienced, rather an interpretation. Yet despite the implications of Bartlett's study, the results have never been successfully replicated by researchers (Gauld & Stephenson, 1967; Roediger, Wheeler, & Rajaram, 1993). In fact, Wheeler and Roediger (1992) observed that after presenting participants with the original 'War of the Ghosts' story memory was *improved* over repeated tests, but only if short delays occurred between the initial study and test. Yet what was important about Bartlett's study was the distinction between Reproductive Memory; referring to accurate production of material from memory, and Reconstructive Memory, emphasizing the process of filling in missing elements, typically with information that is contextually correct, with these distinctions serving as precursors to the episodic and semantic (conceptual) memory outlined in subsequent models (e.g., the CLS model, Squire 1992; McClelland et al., 1995).

Further literature on flashbulb memories has demonstrated that memories for significant world events such as the terrorist attack of September 11th, 2001 are typically reported with high confidence and in high fidelity but are subject to change even within 1 year of the original event and can distort even further over time (Brown & Kulik, 1977; Neisser, 1982, 1986; Lee & Brown, 2003; Conway, Skitka, Hemmerich, & Kershaw, 2009). For example, 50% of participants surveyed in the years after September 11th Terrorist attack report seeing the first plane hit the tower, including then U.S President George W Bush who confidently reported seeing the first plane hit the building, despite the event not being televised (Conway et al., 2009; Greenberg, 2004). These errors are thought to come about through the reorganisation of memory during consolidation adapting information to be consistent with the schema. This effect is often demonstrated in the field of eyewitness testimony. For example, Garcia-Bajos and Migueles (2003) presented participants with an account of a mugging incident containing 10 high typicality actions (e.g., mugger had a weapon) and 10 low typicality actions (e.g., the mugger had a dog with them). In a subsequent recognition task, participants were presented with 20 true/false statements, each containing 5 high/low typicality actions that were reported and 5 high/low typicality actions that were not. In the recognition task participants reported significantly more high-typicality actions, including false recognition of the unstated high-typicality actions, suggesting that prior schema knowledge for the event drove subsequent memory representation, a result that has since been replicated in a series of studies (Aizpurua, Garcia-Bajos, & Migueles, 2008; Garcia-Bajos, Migueles, & Aizurua, 2012). These results suggest that even highly-specific and widely reported events are susceptible to a maladaptive influence of conceptual knowledge, shifting the episodic representation in order to fit in with an expected schema.

In the past two decades the most prominent form of schema-based false memory generation has come in the form of the Deese-Roediger-McDermott (DRM) paradigm (Deese, 1959; Roediger & McDermott, 1995). In Deese's original study, one overlooked until Roediger and McDermott adopted its paradigm, participants viewed a word list then completed a free recall memory task. The primary purpose of the study was to look at extra list intrusions in the free recall. Participants viewed 36 word lists containing 12 words each and each one had a critical associate. For example, the critical word *King* had a word list containing *queen, England, crown, Prince, George, dictator, palace, throne, chess, rule, subjects, monarch, royal, leader & reign.* Deese observed that some lists reliably induced the critical word on immediate free recall. The result of Deese's study was replicated by Roediger and McDermott using six of the critical words from Deese's study. In their study when participants completed a free recall task recall of critical lures (e.g., for the above example, *King*) was extremely high at 55% recall, a result that was higher than words presented in the middle of the study phase and a replication of Deese's original study. When participants were further questioned about the false recall participants regularly responded as having 'known' that the critical word appeared on the original word list. A follow up study by McDermott & Roediger (1998) found that when participants were explicitly instructed to decide carefully whether the critical word had previously appeared the false recall phenomenon still existed. Subsequent research by Neuschatz, Benoit, and Payne (2003) found that only when participants were given an explicit warning on the false memory effect was the effect reduced.

Since its inception the DRM paradigm has been used extensively using both visually and aurally presented word lists to explore various effects, including long-lived semantic priming (McKone & Murphy, 2000), memory illusions (Roediger, 1996), and converging associative networks (Watson, Balota, &

Roediger, 2003). The effect has also been expanded beyond a word list with false memory effects appearing in picture stimuli as well (Roediger, McDermott, & Robinson, 1998; Gallo, McDermott, Percer, & Roediger, 2001; Lutz et al., 2017; Roediger, McDermott, Pisoni, & Gallo, 2004). One recent study, that of Lew and Howe (2016) presented participants with images that contained items that were either schema-consistent (e.g., frying pan on the cooker), schema-inconsistent (e.g., toaster under the table), or schema-irrelevant (e.g., toilet brush on the cooker). In a subsequent recognition task, participants were highly accurate in schema-consistent item locations and schema-irrelevant items, but they observed that schema-inconsistent items were more likely to be falsely recognised as in their schema-consistent locations (e.g., toaster on the worktop), with Lew and Howe theorising that this was in part due to a top-down schema influence on encoding of the episodic memory to make it more consistent with the pre-existing conceptual knowledge. Although it is to my own knowledge the first to explore false memory generation in visual memory in this form, the result is consistent with literature from visual memory. Although it is only recently published the study demonstrates that schema-influence is not limited to just a semantic domain but also visual. Given that these false memory generation effects can occur within an hour of encoding, this suggests that conceptual knowledge has a strong influence on encoding and retrieval of declarative memory, possibly as a result of the expedited consolidation brought about by the items all being consistent within a specific conceptual schema.

1.3.5 Conclusion

To summarise, there appears to be substantial evidence that neocortical representations support a conceptual-schema based model, with examples in this seen across several domains. The role of the conceptual-schema representation is to allow higher-order relationships to form between multiple episodic memories and allow generalisation. Furthermore, there appears to be substantial evidence of a beneficial role of prior knowledge in consolidation of novel information, suggesting that conceptual representations can also affect episodic representations in a form of top-down processing, with conceptual knowledge supporting both encoding through accelerated encoding and retrieval of information through a form of pattern completion. Importantly, it appears that the hippocampus is essential for both initial formation of conceptual knowledge and integration of conceptual representations and episodic, with the hippocampus acting as a form of convergence zone for both new and pre-existing information.

However, there is an unresolved issue: Although there is evidence that pre-existing knowledge can aid specific episodic retrieval, it is unknown what the effect of sleep may have. While recent studies have demonstrated a beneficial effect of sleep on integration of information related to pre-existing knowledge (Hennies et al., 2016), It is unknown what the relation is to episodic representations, similar to that of Konkle et al. (2010a, 2010b). In the following sections I will discuss the role of sleep in regard to the wider literature before focusing more on the role of sleep in abstraction and integration of information.

1.4 Sleep's Role in Memory Consolidation

As previously stated in the introduction to consolidation, the role of sleep in consolidation has been long known, with Marr (1970, 1971) and McClelland et al. (1995) suggesting hippocampal activity during sleep aided memory consolidation. The concept is not a new one, in the 19th century Ebbinghaus (1885) observed recall of newly learned words was improved after a period containing sleep than an equivalent period of wake, leading to the well-established “forgetting curve”. A review almost 50 years later by Van Ormer (1933) found further evidence for the role of sleep in consolidation while other studies such as Patrick (1896) showed the reverse, sleep deprivation led to impaired consolidation. Since then the literature has grown exponentially, with studies demonstrating sleep has a beneficial role in both declarative and procedural tasks (for a summary, see. Diekelmann & Born, 2010; Marshall & Born, 2007; Rasch & Born, 2013). Physiologically, sleep can be divided into stages, rapid eye movement (REM) and non-REM (NREM), which can be further broken down into stage 1 (S1), stage 2 (S2), and SWS (stage 3 and stage 4 combined), with SWS occurring more than REM at the start of the night while this pattern reverses as the night goes on (Figure 1.3). Within the literature there are multiple theories as to sleep's role in consolidation, those that are *stage dependent*, such as the dual process theory and the sequential hypothesis, and those that are more physiologically based, such as the active system consolidation model. Although they are not mutually exclusive, they assume different processes, the former focusing more on the entire sleep stage while the latter is more focused on the neurobiological events within each stage. In the following sections I will discuss these theories, including their strengths, weaknesses, and relevance to the thesis. After discussing the theories I will focus on the role of specific sleep architecture and finally examine the literature on the role of sleep in abstraction and integration of information.

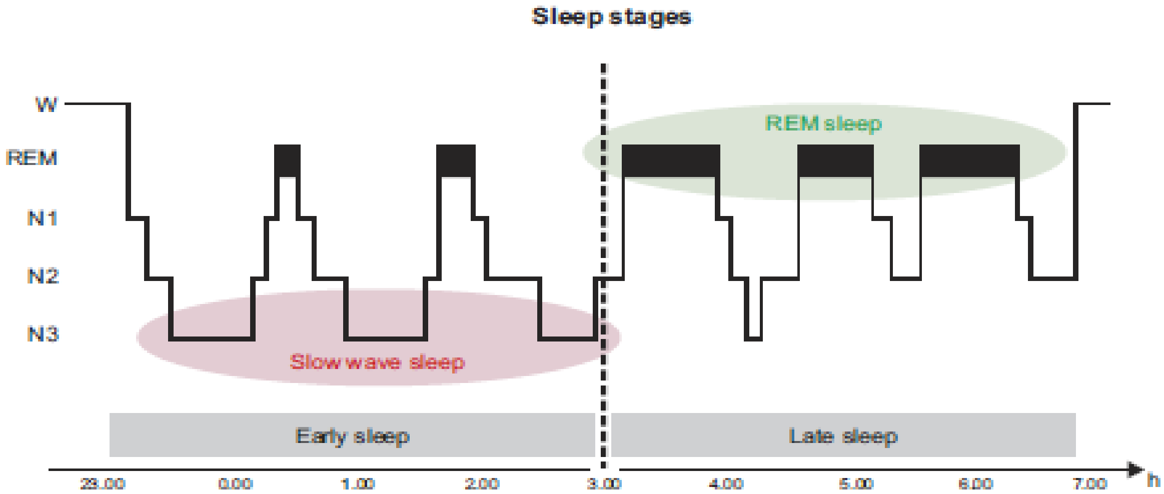

Figure 1.3. Typical sleep stage activity over a single night. Figure taken form Rasch and Born (2013).

1.4.1 Theories of Consolidation within Specific Sleep Stages

1.4.1.1 Dual Process Theory (DPT)

Within the dual process theory of sleep, each specific sleep stage is thought to be beneficial for a memory type, SWS is thought to benefit declarative memory while REM sleep is beneficial for nondeclarative memory. This theory is primarily supported by studies employing the “night-half” paradigm developed by Ekstrand and Colleagues (Yaroush, Sullivan, & Ekstrand, 1971; Fowler, Sullivan, & Ekstrand, 1973; Ekstrand, 1972). Within the paradigm performance is compared across sleep intervals of either the first half or the late half of nocturnal sleep, taking advantage of the SWS dominant first half of sleep and the REM dominated second half to allow comparisons without the confound of repeated awakening. Yaroush et al. (1971) demonstrated the benefit of SWS early sleep compared to REM late sleep in a study on associative word pairs while a study by Barrett and Ekstrand (1972) replicated the effect but controlled for circadian rhythms by manipulating sleep so that both “night-halfs” occurred in the same circadian phase. Plihal and Born (1997, 1999) explored the difference between the SWS-rich early sleep and the REM-rich late sleep further, training participants separately on a word pair task and a separate mirror tracing task. They observed that SWS early sleep was beneficial to the word pairs task while REM late sleep aided the mirror tracing task, supporting the dual process theory (DPT).

While there is strong evidence for the DPT, it has been challenged by some studies. For example, among a host of studies (Aeschbach, Cutler, & Ronda, 2008; Gais, Plihal, Wagner, & Born, 2000; Huber et al., 2006; Huber, Ghliardi, Massimini, & Tononi, 2004). Gais, Plihal, Wagner, and Born (2000) demonstrated a beneficial role of SWS early sleep in a visual texture discrimination task while in the same study Gais et al. also demonstrated a beneficial role of REM late sleep in declarative materials, contradictory to the dual process theory. Another criticism aimed at the theory is that it forgoes a role of sleep stage S2 in any form of memory consolidation, which has been demonstrated to be incorrect (Gais, Mölle, Helms, & Born, 2002; Genzel, Dresler, Wehrle, Grozinger, & Steiger, 2009; Walker, Brakefield, Morgan, Hobson, & Stickgold, 2002; Ruch et al., 2012, van der Helm et al., 2011). For example, sleep after learning a new procedural motor task has been demonstrated to not just increase the time spent in S2, but also the spindle density in S2 (Fogel & Smith, 2006; Fogel, Smith, & Cote, 2007; Nishida & Walker, 2007), with both of these increases correlated with subsequent increased performance in the motor task from pre- to post-sleep. More recently, van der Helm, Gujar, Nishida, and Walker (2011) investigated the impact of sleep on an episodic memory task using an item and context learning paradigm. Within the study participants learned two word lists, each associated with a different context and then assigned to either a nap or no nap group. In a subsequent recognition task they observed that for item memory there was no beneficial effect of sleep, but for context memory, which is hippocampal dependent, there was a significant benefit of sleep, with accuracy significantly correlating with amount of S2 sleep, a result supported by Ruch et al. (2012) who demonstrated S2's role in consolidation of declarative memories. In Ruch et al.'s (2012) study, participants learned associations between faces and cities and after a nap completed a cued recall task, with sleep stages and spindle activity monitored during sleep. Increases in spindle activity in S2 were associated with enhanced retention of face-city associations.

1.4.1.2 Sequential Model of Sleep

As an alternative, the sequential model of sleep was proposed, suggesting the cyclic nature of REM and NREM across the sleep cycle was important for consolidation (Ambrosini & Guiditta, 2001). Early evidence in support of this model includes the previously mentioned study by Gais, Plihal, Wagner, and Born (2000). In a visual discrimination task Gais et al. observed that SWS had a beneficial role in the consolidation of visual information alongside a REM-based beneficial role in declarative memory. Interestingly, they observed that when participants completed the full sleep cycle, going through SWS and REM multiple times performance increased significantly, strongly supporting the concept that sequential sleep may be more beneficial than any one stage. Elsewhere, retention of verbal material has been correlated with both early SWS and late REM, again supporting the view that repeated cycles are more important than any one stage (Ficca, Lombardo, Rossi, & Salzarulo, 2000; Mazzoni et al., 1999). The sequential hypothesis has even been supported by nap studies: A study by Mednick, Nakayama, and Stickgold (2003) observed that discrimination thresholds in the same task only improved after a nap containing both NREM and REM sleep but not just NREM. All of these studies suggest that the sequential hypothesis appears more consistent with the literature than the dual process theory.

As with the DPT, there are issues with the sequential hypothesis. Issues regarding the methodology of fragmenting participants' sleep in order to measure results and that these rely upon correlations between sleep stages and results allow no causal link to be examined. While it may be the more useful model in terms of explaining the role of sleep stages, it is still lacking testability. In an effort to seek a more in-depth view of the process, theories such as the Active System Consolidation (ASC) model instead more towards a more biological focus, focusing on the specific sleep architecture and cortical events that occur during sleep stages and how they may contribute to consolidation.

1.4.1.3 Active System Consolidation Model

Building upon the existing literature, the underlying theory of the ASC model integrates both dual process theory and the sequential hypothesis but adopts a more architecture-based view, looking at specific sleep architecture occurring during stages rather than the overall stage. During SWS, slow oscillations drive memory consolidation through repeated activation of newly encoded memory representations within the hippocampal stores, driving gradual redistribution to the neocortical store. This gradual redistribution results in a qualitative shift in the memory representation as outlined in the CLS model of consolidation (Squire, 1994; McClelland et al., 1995), moving from a veridical based representation to a more semantic, “gist” representation that allows long-term storage. Subsequent periods of REM sleep are thought to act as a period of stabilisation through synaptic consolidation. The important distinction from this and previous models is the focus on the interaction between three aspects of sleep architecture, slow wave activity, hippocampal sharp wave ripples, and sleep spindles (Rasch & Born, 2013). In the following section I will review each of these aspects in more detail and linking them to sleep-based consolidation.

1.4.2 Sleep Architecture

Slow Wave activity

During SWS EEG activity is primarily Slow Wave Activity (SWA). Defined as 0.5-4Hz frequency and <1Hz oscillation, SWA has been demonstrated to play a significant role in consolidation of memory. In animal studies learning new information has led to increases in SWA in subsequent SWS (Kattler, Dijk, & Borbely, 1994; Vyazovskiy, Borbely, & Tobler, 2000), with hemispheric differences observed depending on which paw the rat used during the day (Vyazovskiy, Cirelli, Tononi, & Tobler, 2008). This pattern has been repeated in humans, with Gais, Wagner & Born, (2002) observing increases in SWA during sleep stage SWS after a period of learning word pairs. Furthermore, several studies using transcranial direct current stimulation (tDCS) has provided direct evidence for a causal role of SWA in consolidation. Marshall, Helgadottir, Mölle, & Born (2006) applied tDCS to induce slow oscillating field potentials over the pre-frontal cortex during NREM sleep and observed an increase in SWA that subsequently produced a significant improvement in retention of word pairs. At the other end of the scale, applying tDCS at 5Hz had a suppressing effect upon the SWA affecting performance on the retention task (Marshall, Kirov, Brade, Mölle, & Born, 2011). Although this research direction is relatively new, dating back only the last decade, these studies demonstrate a direct causal role of SWA and SWS more generally in the consolidation of memory during sleep.

Hippocampal Sharp Wave Ripples

As stated in section 1.1 of the literature review, a key point of the CLS models is the role of sleep in consolidation; sleep is thought to be a period of offline consolidation where repeated activation of hippocampal representation leads to a hippocampal-neocortical transfer. Advances in neuroimaging have revealed a wealth of evidence supporting hippocampal reactivation during sleep in both animal and human studies. Hippocampal SW-R are primarily composed of large amplitude sharp waves in local field potentials and are suggested to be indicators of the most prominent hippocampal activity and are suggested to play an essential role in consolidation. One study that demonstrated their importance was that of Girardeau, Benchenane, Wiener, Buzsaki, and Zugaro (2009) who interfered with hippocampal ripples in sleeping rats who learned a spatial navigation task. Those rats whose hippocampal ripples were not modified had no issues with the task after a period of sleep. In contrast, those whose hippocampal ripples were blocked learned at a slower rate and did not achieve an equivalent level of performance. This result was repeated by Ego-Stengel and Wilson (2010) who trained rats in two identical special navigation task. In the 1h rest period after the experimental task, the rats experienced disruption of hippocampal SW-R. In a subsequent task, performance in the control task was significantly faster than the task followed by hippocampal interference, indicating hippocampal ripples are important for consolidation and learning. As previously stated, these hippocampal SW-R are often temporally synchronised with spindles. Intracranial recordings from rats and humans have observed that SW-R are associated with a rise in spindle activity shortly before the ripple onset and that outlast the ripple (Mölle, Yeshenko, Marshall, Sara, & Born, 2006), with Mölle, Eschenko, Gais, Sara, and Born (2009) observing that during sleep following a learning task spindle activity increased further. Furthermore, temporal analyses reveals that spindles and ripples lead to a “spindle-ripple event”, whereby individual ripples become temporally nested in repeated troughs of a spindle (Siapas & Wilson, 1998; Wierzenski, Lubenov Gu, & Siapas, 2009). Taken together, these events may represent the CLS’s suggested transfer of reactivated memories from the hippocampus to neocortical sites (Sirota & Buzaki, 2005; Mölle & Born, 2009).

Sleep Spindles

One of the more recent areas of research in the sleep literature is the role of sleep spindles in memory consolidation. Sleep spindles are characterised as small bursts of activity (11-15Hz) that are relatively fast, typically lasting anywhere between 0.5 – 3s (De Gennaro & Ferrera, 2003). Spindles are most prominent during S2 but are also detectable during SWS, with spindle frequency gradually decreasing as SWS processes (Andrillon et al, 2011; Azumi & Shirakawa, 1982; Dijk, Hayes, & Czeisler, 1993; de Gennaro & Ferrara, 2003; de Gennaro et al, 2000; Marshall, Mölle, Hallschmid, & Born, 2004; Silverstein & Levy, 1976; Uchida, Atsumi, & Kojima, 1994; Zeitlhofer, 1997). Moreover, spindles are of particular interest due to their temporal synchronisation with hippocampal sharp-wave ripples (SW-R) (e.g., Siapas & Wilson, 1998; Clemens, Mölle, Eross, Barsi, Halaz, & Born, 2007; for a summary, see. Rasch & Born, 2013). While studies have linked spindle activity to IQ (Nader & Smith, 2001; Schabus et al. 2004), many studies in the field of behavioural psychology have demonstrated a strong relationship between sleep spindles and offline memory consolidation during sleep for both declarative and procedural learning. For example, several studies have demonstrated that spindle activity is linked to performance in spatial navigation tasks (Meier-Koll, Bussmann, Schmidt, & Neuschwander, 1999), motor learning (Fogel & smith, 2006; Fogel, Smith, & Cote, 2007; Nishida & Walker, 2007; Tamaki, Matsuoka, Nittono, & Hori, 2008; 2009), item-context pairs (Ruch et al., 2012; van der Helm et al., 2011), face-name associations (Clemens, Fabo, & Halasz, 2005), and word-pair learning (Gais, Mölle, Helms, & Born, 2002; Schabus et al., 2004; Schmidt et al., 2006; Schabus et al., 2008). One key study in recent years was that of Tamminen, Payne, Stickgold, Wamsley, and Gaskell (2010) who looked at spindles in relation to item integration. Within the study participants learned novel spoken words that had phonological overlap with existing vocabulary (e.g., *cathedruke-cathedral*) then were either in a wake group or a sleep group that was monitored via polysomnography, with a recall test after the delay and a second recall test one week later. Tamminen et al. observed that participants in the sleep group recalled more words and recognised them faster than the wake group in the 12h delayed test, with the wake group only reporting similar accuracy and speed after the one week delay. Furthermore, recognition of existing vocabulary significantly slowed in both groups after the retention interval, suggesting that novel words had become consolidated and acted as interference for the existing vocabulary. More relevant to the current section, increased spindle activity was strongly correlated with overnight lexical integration of novel words but this was not reflected in increases in recall rate or recognition speed of the novel words, suggesting a central role of spindles in the consolidation and integration of newly learned material into existing cortical networks.

It is also important to note that spindle activity has been linked to region-specific locations for memory consolidation. Previously, Nishida and Walker (2007) demonstrated region-specific spindle activity with relation to a procedural memory task. Participants were trained on a finger tapping task using their left hand and in a subsequent nap period Nishida and Walker observed a significant increase in spindle activity that correlated with performance improvement. When examined further, this correlation was due to spindle activity specifically in the contralateral (right) motor area, with no correlations observed for the LH, suggesting spindles are linked to region-specific consolidation rather than a global effect. Further evidence of this can be seen in a study by Tamminen et al. (2013)

who examined the role of spindles in the integration of novel words into densely or sparsely populated semantic neighbourhood. Within the study participants learned novel words over two sessions and recall was measured immediately after training, the following morning, and one week after. They observed that although recognition amount was equal across both conditions, novel words from the dense semantic neighbourhood were significantly lower in recognition, with Tamminen et al. taking this as evidence for integration of the novel words into the existing semantic network with existing vocabulary acting as interference. They also observed that spindle activity was linked to semantic density, with the sparse semantic neighbourhood related to more sleep spindles during sleep than the dense semantic neighbourhood. Critically, they observed a significant interaction between neighbourhood and hemispheric spindles; the neighbourhood effect observed was specific to the left hemisphere. The result appears consistent with current theories that sleep aids integration of recent experiences into the long-term vocabulary store (Dumay & Gaskell, 2007, 2012) which is suggested to be located in the LH (Ellis, 2004; Ellis et al., 2009). The relevance of hemispheric lateralisation in sleep will be discussed further in Chapter 5.

Yet there is an important point to make about the previous paragraph, the spindle ripple events observed are restricted to *fast* spindles. Studies have demonstrated two types of spindles; fast spindles (13-15Hz) are typically distributed over the central and parietal cortex and are typically in S2 whereas slow spindles (10-12Hz) are primarily concentrated around the frontal cortex and are more pronounced in SWS (Anderer et al., 2001; De Gennaro & Ferrara, 2003; Mölle, Bergman, Marshall, & Born, 2011; Terrier & Gottesmann, 1978). Importantly, the two spindles are also associated with different areas of activity; slow spindles with increased activation in the superior frontal gyrus whereas fast spindles are associated with activation in the hippocampus, suggesting a relationship between fast spindles and hippocampal-dependent memory processes. Recent literature exploring this different has demonstrated key differences. Schimdt et al. (2006) observed that compared to a non-learning task spindle activity increased after learning word-pairs, and more specifically, only for slow spindles in frontocentral areas. In the study by van der Helm et al. (2011) within the recognition task they observed that for item memory there was no beneficial effect of sleep, but for context memory, which is hippocampal dependent, there was a significant benefit of sleep, with accuracy significantly correlating with both amount of S2 sleep and frontal fast spindle density. This effect is not limited to declarative memory, with Tamaki et al. (2008, 2009) observing an increase in fast spindle activity following a visuospatial motor task but no such increase for slow spindles. These studies suggest that fast spindles in particular may be vital for neocortical consolidation and links to hippocampal activity.

1.4.3 Sleep’s role in consolidation- Abstraction and Integration

In the last few decades a wealth of literature has demonstrated that sleep is a factor in promotion of associative and a conceptualised form of memory (for a summary, see Chatburn et al., 2014, Mirkovic & Gaskell, 2016), with sleep benefitting consolidation of numerous forms of abstraction. In a study on relational memory, Ellenbogen Hu, Payne, Titone, and Walker (2007) taught participants a series of premise pairs (A>B, B>C, C>D, D>E, E>F), with an embedded hierarchy (A>B>C>D>E>F). After a delay of 20 minutes, 12 h containing sleep/wake, or 24h participants were examined in an inferential judgement task for novel pairs (e.g., B>D, C>F, B>E). They observed that while the original premise pair recognition was consistent across all groups, only those who had a period of offline delay displayed inferential ability in the novel pair task, suggesting that sleep appears to preferentially facilitate inferential processes through enhancing hierarchical memory. This was expanded upon by Sio, Monaghan, and Ormerod (2013) who demonstrated a similar effect in problem solving. Participants were presented with a set of remote-associate tasks of varying difficulty and after a period of sleep or wake reattempted unsolved problems. They observed that participants in the sleep group completed a greater number of problems than other groups, but this only applied to problems categorised as difficult, with no difference in easy problems, a result consistent with existing literature (Cai et al., 2009; Kuriyama, Stickgold, and Walker, 2004). The beneficial role of sleep in abstraction has even been demonstrated in infants, with Gomez, Bootzin, and Nadel (2006) observing that 15-month-old infants who napped between familiarisation and test on an artificial language appeared to remember more abstract relations in the language and generalised to stimuli similar to the familiarisation task. Efforts to create theoretical accounts of abstraction and integration during sleep have resulted in two prominent theories; *the Memory Triage model* by Stickgold and Walker (2013) and the *information Overlap to Abstract* (iOtA) model by Lewis and Durrant (2011). In understanding how sleep can lead to abstraction and integration of information, these theories can be broadly split into two key processes: how memory selection occurs during sleep, and how memory reactivation during sleep can affect consolidation.

Memory Selection

In order to avoid consolidating superfluous information consolidation processes during sleep must be capable of preferentially selecting which memories are consolidated and which aren't. Task salience has been denoted as an important factor in this area, with the nature of the task being implicit or explicit demonstrated to affect subsequent post-sleep retention (Song, 2009; Spencer, Sunm, & Ivry, 2006). Task salience doesn't even have to be explicit at the time of encoding but can be revealed any time before sleep. Fischer and Born (2009) noted that sleep can selectively consolidate memory based on a potential reward upon waking, even after only being told of a future reward after learning, suggesting we can engage in selective preservation, possibly linked to the previously mentioned top-down processing that the neocortical conceptual knowledge can influence episodic representations.

Memory Reactivation

A key assumption of the ASC model is that during sleep memory representations are repeatedly reactivated and this in turn leads to consolidation. Evidence of this can be seen in the work of Wilson and McNaughton (1994) who recorded hippocampal CA1 place cells in rats during a physical activity to earn food. In subsequent SWS the hippocampal firing pattern was similar to that of the rat performing the action when awake, with the pattern not seen in sleep preceding the action. This pattern has been demonstrated in numerous species including primates (Hoffman & McNaughton, 2002) and birds (Dave & Margoliash, 2000). In humans, Peigneux et al. (2004) observed clear signs of hippocampal reactivation during SWS in participants who learned a spatial navigation task with the size of hippocampal reactivation predicting performance at a later retest. This and subsequent studies suggest that during sleep the neuronal firing pattern during wake is replayed, albeit in a compressed form (Lee & Wilson, 2002). More recently, Deuker et al. (2013) were able to provide evidence of reactivation of specific memories during sleep, with Deuker and colleagues observing specific patterns that were identified during memory encoding reoccurring during post-learning sleep.

Further studies have demonstrated hippocampal reactivation during SWS through cueing. Rasch, Buchel, Gais, and Born (2007) had participants learn card-pair locations alongside a specific odour cue (e.g., *roses*). When participants entered SWS the odour was presented again and in subsequent recall task participants recalled significantly more card-pair locations, with fMRI confirming hippocampal reactivation during odour exposure and more interestingly, actually increased hippocampal activation compared to wake. Ensuing studies have demonstrated this isn’t limited to just odour cues, with Rudoy, Voss, Westerberg, and Paller (2009) demonstrating that sounds can also benefit hippocampal reactivation in SWS.

As discussed in the previous sections, promotion of a conceptual-schema driven process can also lead to false memories. Within the sleep literature there is a growing consensus of the role of sleep in false memory generation. Using the DRM paradigm one of the first reported studies, that of Diekelmann, Landolt, Lahl, Born, and Wagner (2008) reported false memory generation as a result of sleep *deprivation*. Within a series of experiments participants were exposed to a series of DRM wordlists and were either sleep deprived, sleep through the night, or had an equivalent period of wake then completed a recognition task on seen words (old), unseen words (new), or unseen but related words (critical lure). There was no significant difference between the sleep or day-wake group, suggesting no role of sleep in the consolidation of false memories, but those in the sleep deprivation group recognised significantly more critical lures than either group. The lack of a sleep effect in generation of false memories was repeated by Fenn et al. (2009) who utilising the same methodology demonstrated that sleep *reduced* false recognition of lure words, extending the results that sleep is beneficial to episodic memory. The growing literature that sleep has no or a reducing effect on false memories was contradicted by Payne et al. (2009). Within their study participants were exposed to DRM lists just like Diekelmann et al. and Fenn et al. but memory was measured by recall instead of recognition. When measured by recall sleep was found to increase false memory generation compared to an equivalent period of wake, with the results also replicated in a nap study. Moreover, Payne et al. were able to link false memory generation to sleep architecture; within both the overnight and nap paradigms SWS was significantly *negatively* correlated with recall accuracy, r = -0.60 and r = -0.54 respectively. As with other studies, the false memory generation during sleep does appear to suggest that conceptual knowledge is promoted during sleep. Although the exact mechanisms are unclear there are models that seek to explain it. The following sections will explore these models further.

Memory Triage Model of Sleep-based Consolidation

Within the literature there are multiple models for conceptual-schema based consolidation. One such theory is that of Stickgold and Walker's (2013) *Memory Triage* model. Underlying the model is that memory consolidation is not universal, instead memories are filtered for which will be retained and in what form to be consolidated. There is some evidence for the former; emotional memory has been demonstrated to undergo preferential preservation during REM sleep (Hu, Stylos-Allan, & Walker, 2006; Atienza & Cantero, 2008; Nishida, Pearsall, Buckner, & Walker, 2009; Wagner, Gais, & Born, 2001; Wilhelm, Diekelmann, & Born, 2008) while others have demonstrated sleep can selectively consolidate memory based on a potential reward upon waking, even after only being told of a future reward after learning (Fischer & Born, 2009), suggesting we can engage in selective preservation. Following on from memory discrimination items can be consolidated in two possible ways, item integration or multi-item generalisation. Within item integration the newly learned representation can be consolidated into pre-existing schema, with the schema's rules expanding upon integration. Example of this form of consolidation can be seen in the work of Dumay and Gaskell (2012) and Tamminen et al. (2010) in the *cathedruke-cathedral* paradigm. To recap these studies, participants learned a novel word similar to an existing vocabulary item and after sleep there was evidence of the novel word becoming integrated into the existing vocabulary store. Similarly, the results of Sio et al. (2013) can be explained by this concept. Item integration of the remote-associate tasks into existing categorical networks prompted new associations to form, resulting in a subsequent increase in performance. The second form of consolidation, the multi-item generalisation can also account for the previously discussed studies. Gomez et al.'s (2006) observation that 15-

month-old infants were able to engage in abstraction and rule extraction support the concept of sleep actively creating cognitive schemata based on new information, as does Ellenbogen et al.'s (2007) observation of sleep aiding relational memory.

iOtA model of Sleep-based consolidation

However, an issue with Stickgold and Walker's (2013) model is that although it can account for much of the observed effects of sleep, the functions provided are not strictly limited *to* sleep, and as such it raises questions as to its suitability for explaining sleep based associative consolidation. An alternate theory is promoted by Lewis and Durrant (2011). Within their model, the information Overlap to Abstract (iOtA), abstraction of rules can be explained through repeated reactivation of memories and their influence on existing schemata. As previously mentioned, there is recent literature suggesting that hippocampal-neocortical transfer occurs faster in cases where the encoded representation is compatible with existing schemas (Tse et al., 2007; van Kersteren et al., 2010a, 2010b). Building upon this and existing models of consolidation such as the CLS (Squire, 1992; McClelland et al., 1995; Winocur et al., 2010), Lewis and Durrant suggest that in initial consolidation all connections between memories are activated but during sleep as repeated reactivation of hippocampal representation occurs, connections between common features/themes will become stronger than the single unified memory. With each repeated reactivation during SWS, the overlapping features are 'primed' for the following reactivation, resulting in a strongly consolidated gist based representation that encapsulates common features of multiple memories. While this has a clear advantageous effect, benefitting abstraction of information and building cognitive schemata, it does explain the recent literature that suggests promotion of gist based consolidation during sleep may lead to subsequent false memory errors during retrieval (Pardilla-Delgado & Payne, 2017; Payne et al., 2009).

1.4.4 Role of Pre-Existing Conceptual Knowledge in Sleep

Recently, an exciting strand of literature has sought to examine the role of pre-existing conceptual knowledge and how sleep may affect consolidation of related material. Much of this stems from the work of van Kesteren and colleagues van Kesteren, Rijpkema, Ruiter, & Fernández, 2010; van Kesteren et al., 2013; van Kesteren, Fernández, et al., 2010) and the development of the *Schema-Linked Interactions between Medial prefrontal and Medial Temporal regions* (SLIMM) model, which proposes that when information is perceived as congruent to an existing schema, a mutual-reinforcement activity occurs across the cortical network associated with the schema. Related to sleep, van Kesteren et al. (2010) presented participants with incongruent and congruent item-background pairs and observed that sleep preferentially consolidated information that was congruent with preexisting schema. Within audio stimuli, Durrant, Cairney, McDemott, and Lewis (2015) required participants to learn a series of melodies, half of which conformed to a tonal schema, and half of which did not. After a 24h consolidation period participants were presented with more melodies, before completing a recognition test where melodies from both sessions were presented alongside unheard foils. Durrant et al. (2015) observed that participants remembered the schema-conformant melodies better than non-conformant melodies, suggesting that over a 24h consolidation period schema-consistent items are preferentially consolidated; moreover, analysis of the participants data revealed a correlation between consolidation and REM sleep, adding to previous literature that favours a link to SWS. Within a linguistic domain, the aforementioned Tamminen et al. (2010, 2013) studies provided evidence that during sleep information can become integrated into existing knowledge structure, with sleep spindles in particular linked to consolidation. Building upon this, Hennies et al. (2016) sought to explicitly link sleep architecture to consolidation within pre-existing conceptual knowledge. Within the study participants were trained on a schema over the span of 2 weeks in order to establish a schema. Once a schema had been established participants encoded new facts that were either schema-related or schema-unrelated. After a 24h delay containing a period of sleep monitored with polysomnography participants encoded a second set of facts with a 2AFC task on all 144 facts occurring shortly after. Hennies and colleagues observed that spindle density predicted an increase in schema benefit to memory over the retention interval, with the higher spindle densities associated with reduced decay of schema-related memories. These studies provide evidence that sleep is associated with the interaction between pre-existing conceptual knowledge and long-term memory formation.

1.5 Overview and Objectives of the Thesis

Throughout the thesis the aim is to understand the role of sleep in complex, multi-item episodic memory. More specifically, I seek to expand on the literature that suggests the hippocampus is a ‘convergence zone’, acting as a site where bound representations (multiple items stored as one representation, e.g., a representation of a classroom features many items) can be formed (for a summary, see Horner & Doeller, 2017) and how conceptual knowledge and sleep may interact in this. In the previous literature, most of the investigations into this are primarily through associative cues, participants learn an associative pairing or a complex-multi-item event (called bound representations in subsequent chapters) then in subsequent recognition or recall tasks part of the learned association is presented and successful retrieval of the other half suggests a bound representation. Within the thesis I seek to extend this to specific bound representations when presented in a two-alternative-forced-choice task. Within this form of recognition paradigm it requires a stronger bound representation as participants are presented with both the target bound representation and an alternative foil that may contain similar/competing items with recognition requiring the specific pairing.

First, as the previous literature has focused primarily on testing and developing theories from a mono-cultural (Western) sample, as a validation of previous research (e.g., Urgolites & Wood, 2013b), Experiment 1a focused on the role of culture in associative memories to see if issues related to bound representations in visual long-term memory is a cross-cultural effect and not specific to Western participants, Experiment 1b sought to determine whether effects were due to familiarity or due to differences in binding, and Experiment 2 utilised different stimuli (object-scene and action-scene) to ensure any observed effects were not unique to one form of stimuli .

Within Chapter 3, the role of sleep is examined in bound representations within visual long-term memory. Participants in either a sleep (9pm-9am) or wake (9am-9pm) group were tested on their ability to recognise specific action-scene and object-scene composites. Alongside this study separate control studies were conducted with the same stimuli in order to ensure no confounding effects of circadian rhythm. In Chapter 4, as some literature has suggested that context can aid retrieval of visual information (e.g., Kersten, 1988), sleep's role in visual long-term memory was investigated in a contextualised setting; instead of using unrelated action-scene or object-scene composites CCTV videos of crimes were displayed and retrieval for the different item modalities measured in a recall task in order to see if pre-existing conceptual schema promoted any item modality over another. Chapter 5 shifts stimuli to that of DRM wordlists, previously demonstrated to promote false memories. Within the study, participants were presented with several DRM wordlists and then were either awake or had a nap (90 mins) that used polysomnography to record sleep stages and sleep spindles. Within the recognition task participants were presented with old, new, and critical lure words from the DRM lists to either hemisphere in order to account for existing hemispheric semantic networks (Beeman, 1998; Beeman & Bowden, 2000). Finally, in Chapter 6 the main results and themes of the experiments are discussed within the wider literature, where future studies can go, and methodological issues that occurred.

Chapter 2. Impact of Culture in the Relaional Binding of Actions, Objects, and Scenes in Visual Long-Term Memory

Before examining the role of sleep of associative memory in the VLTM there is an important methodological point that was noted during the literature review. The past literature on the VLTM has demonstrated that humans have a remarkable capacity for visual items, with studies demonstrating that in recognition tasks participants can recognise objects, scenes, and actions, even when over 2500+ images have been presented. Moreover, these aren't low fidelity representations, with studies with multiple category level exemplars replicating this effect, suggesting the VLTM is capable of storing a large quantity of high-fidelity visual representations. However, recent literature in cross-cultural psychology has suggested differences in perceptual processing between East Asian cultures and Western cultures, the latter of which the VLTM literature is focused on. These differences can manifest as early perceptual differences as well as differences in recall and recognition. As universities are a now a lot more international, it is important to explore in any potential effect of culture in order to account for any potential confound in subsequent studies.

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Abstract

The degree of individualism or collectivism in a culture has observable effects on cognitive processing. Participants from collectivist cultures are less able to identify a previously displayed object when presented with a novel background than participants from individualist cultures. This can be interpreted as collectivist cultures more likely to process information field dependently. We tested explicitly whether collectivist or individualist cultures are more likely to bind foreground and background images and whether such binding is differentially affected for object-scene and action-scene combinations. Across three experiments participants viewed item-context composites, then completed a forced-choice recognition task. In Experiment 1, 61 UK and 57 Malaysian participants viewed object-scene composites, with UK participants significantly more accurate in correct composite recognition, with Experiment 2 demonstrating this difference was not due to cultural differences in object familiarity. In Experiment 3, 62 UK and 67 Malaysian participants viewed action-scene composites, with no significant difference between cultures in proportion of items recognised. The results of Experiment 1 suggest that the UK sample were able to store high-fidelity representations of visual features as an association between item and context, while the Malaysian sample were unable to. This result is discussed in relation to both cultural, and cognitive psychology.

Keywords

Culture, Visual Long-Term Memory, Binding Memory, Item-Context Recognition

Highlights

- Western participants are more accurate in recognition of specific object-scene bound representations
- Across both cultures bound representations that only altered the background were significantly more likely to be recognized than bound representations that only changed foreground, or both elements

1. Introduction

In the field of culture, a large number of studies have suggested there are differences between Western and East Asian cultures. Westerners are thought to engage in analytical processing, focusing on salient objects, while East Asian cultures engage in holistic processing, focusing on processing scenes within context. This difference has been suggested to be due to Western cultures typically being more individualist while East Asian cultures are typically more collectivist (Gutchess et al., 2006, Masuda & Nisbett, 2001; Na et al., 2010; Nisbett; 2003; Nisbett & Masuda, 2003). Within these studies, American and Japanese participants view a focal object in a scene (e.g., fish in a pond), and after a delay recognition of the focal objects are tested with visual scenes manipulated so that old objects may be presented in an old or new background, or a new object may be presented in an old or new background, with participants completing a Yes/No (YN) recognition task on the focal object (Chua, Boland, & Nisbett, 2005; Masuda & Nisbett, 2001). In a seminal paper, Masuda and Nisbett (2001) reported that Japanese participants were more likely to describe previously seen video clips contextually than American participants who focused more on foreground details. Likewise, in speeded recognition tasks Japanese participants were more accurate when the target object is presented in the same training context whereas American participants were unaffected by the contextual manipulations but were overall slower than East Asian participants when identifying the focal object in all conditions. This difference based upon culture was suggested to be evidence of decontextualisation (analytical processing) in American participants and binding (holistic processing) in Japanese participants; Americans were slower due to processing the object and background separately, whilst Japanese participants were quicker due to the holistic binding, but at the cost of reduced accuracy when the context changed. Follow up studies ultilising a change-blindness paradigm (where participants are required to identify changes in either foreground or background) also observed that East Asian participants were much more attentive to contextual changes while American participants were more attentive to focal object changes (Masuda & Nisbett, 2006). This is further expanded upon in the culture-based attentional bias theory that suggests that Americans are better than East Asians at detecting changes in the centre of the screen, suggesting that East Asians allocate their attention more broadly (Boduroglu et al., 2009). Within the theory, there is some evidence that culture influences early attention (Chua et al., 2005; Goh et al., 2009; Ji et al., 2000; Kitayama et al., 2003) with American participants looking at central objects sooner and longer than East Asian participants, who made more saccades to the background, suggesting East Asians allocate attention more broadly than Westerners. This results in greater detection in changes to contextual stimuli but at the expense of reduced reaction time for changes in focal objects, supporting the interference effect of novel backgrounds in Masuda and Nisbett's (2001) study although this has been disputed in some eye-tracking studies that have found no effect on culture on saccades (Evans et al., 2009; Rayner et al., 2007).

Although these studies have demonstrated cultural differences in visual recognition, much of the focus has been on how context can affect recognition of a focal object, with little research on the recognition of the context itself. At present only one study has looked at this: Millar et al. (2013) investigated the influence on culture on separate foreground and background recognition. In their first experiment, participants were shown objects or backgrounds and in a subsequent recognition task were shown the original image, a similar image, or a new, foil image. In a second experiment, the object and background were shown in a composite image before a recognition task displayed the items separately, with recognition scored as either specific- (seen for old items, not seen for similar), or general- memory (seen for old items and similar items. It was observed that Americans exhibited greater accuracy in specific memory compared to East Asians, while both cultures performed similar on measures of general memory, with this pattern observed across both object and background recognition. From this, Millar et al. suggested that Western culture's analytical focus means individuals are more likely to study specific details of focal objects, whilst East Asian cultures, by focusing on the holistic image, miss these specific details but have a general recognition similar to Western participants. The result appears consistent with the visual long-term memory literature that has largely focused on Western participants, with recent research on image recognition demonstrating humans have a remarkable ability to recognise visual items, with scene (Konkle, Brady, Alvarez, & Oliva, 2010), object (Brady, Konkle, Alvarez, & Oliva, 2008), and action (Urgolites & Wood, 2013a) recognition observed to accuracy levels above 80%, suggesting that we are able to store high-fidelity representations of previously seen stimuli.

However, when expanded to specific item-context composite memory, where an action- or object- scene composite image is displayed and participants have to recognise that specific pairing (e.g., a man performing a twist in front of a harbour), proportion of items correctly recognised in Western participants drops significantly in two alternative forced-choice (2AFC) tasks to close to chance (Urgolites & Wood, 2013b). The result is more surprising as with the same composite stimuli, participants are able to recognise an individual element of the composite close to previously reported accuracy levels, again supporting Millar et al. (2013). These results suggest that while Western participants are capable of binding visual stimuli together, this process is difficult and prone to errors in spite of participants having a detailed memory of the individual elements.

The result can be interpreted within theories of recognition, for example, dual process theory of recognition memory assumes recognition can be split into two facets, familiarity and recollection, analogous to the general- and specific-memory split suggested by Millar et al (2013). Familiarity is considered an automatic process that allows recognition but no retrieval of specific detail, while recollection requires a conscious effort of specific details related to the encoding episode, requiring a longer processing time, with both suggested to rely upon different memory traces (for a summary, see Yonelinas, 2002, 2010; Zimmer et al., 2006). Familiarity is suggested to rely on an object 'token'; information about the object such as colour, size, and shape, while recollection requires an episodic token, integrating the object-token with additional contextual information, allowing the 'where, when, how' questions to be answered (for a summary, see Ecker et al., 2004). When applied to the results observed in the culture literature, it appears that Western participants employ recollection, as demonstrated in Millar et al. and this theory can be interpreted as a potential explanation for the longer reaction time in Masuda and Nisbett (2001). East Asian cultures that rely on familiarity based recognition due to holistic processing would typically be quicker in their reaction times, but less accurate on specific recognition tasks, again as seen in Masuda & Nisbett.

Although this is a suitable explanation for the item- or context-recognition, it is unable to account for the accuracy in specific item-context composite recognition. One theory, suggested by Chalfonte and Johnson (1996) suggest there are at least two ways that feature binding may be expressed. Features may be independently represented, but associated or features may form a blended representation, distinct from the two features separately (Chalfonte & Johnson, 1996; Graf & Schacter, 1989). When applied to culture-based visual recognition, it appears that Western participants employ this independent but associated representation, as demonstrated by the existing literature, while East Asian cultures rely on blended representation, with this distinction supported by the existing cultural literature (Gutchess et al., 2006, Na et al., 2010; Nisbett; 2003; Nisbett & Masuda, 2003; Masuda & Nisbett, 2001), although it has not been explicitly tested in a specific composite memory task. As such, within the current study, we sought to examine whether there is a significant cultural difference between Western (UK) and East Asian (Malaysian) participants in recognition of specific item-context composite videos that can relate to this proposed difference in feature binding.

In order to ensure it was only specific item-context composite memory being tested, recognition was measured by a 2AFC task rather than a YN recognition task. While previous studies utilized a YN recognition paradigm (Chua et al., 2005; Evans et al., 2009; Masuda & Nisbett, 2001; Millar et al., 2013; Rayner et al., 2007), when the YN task is compared to 2AFC recognition tasks, performance on 2AFC is reliably better due to its performance being determined by the proportion of correctly identified items, minimizing false alarm rates from noise trials observed in the YN recognition task (Jiang, Wixted, & Huber, 2009). Furthermore, the same study observed a difference between Forced-Choice Corresponding (FC-C) and Forced-Choice Non-Corresponding (FC-NC). FC-C involves the target item being paired with a similar foil in order to generate similar levels of familiarity but stronger in the target item.   As such, the familiarity may initially generate a high number of false alarms but recognition of the specific composite image should lead to a reliable difference throughout testing (Jiang et al., 2009). As such, the current study used a 2AFC paradigm with three types of foil, two FC-C and one FC-NC, with all visual components taken from previously existing stimuli but in novel composites in order to ensure it was specific binding memory that was being tested.

In accordance with Chalfonte and Johnson's (1996) feature binding theory, we hypothesized that the Western participants would more accurately recognize specific object-scene composites compared to the East Asian participants due to Westerner's analytical processing supporting associated, high-fidelity visual representations compared to the East Asian's holistic processing supporting reduced fidelity, blended visual representations, making recognition more susceptible to the FC-C foils. In order to minimize any cultural effects of visual novelty, such as those demonstrated in Goh et al. (2009), The foils used in the testing phased contained stimuli already seen in the training phase but in new pairings to avoid novel visual information. Whereas previous studies have focused upon a largely Chinese/Japanese based participant group, this study has focused upon Malaysia, due to Malaysia being an Asian culture but using a Latin-based language as well as a high English speaking population. This population should account for de-confounding any potential effects a pictographic-based language, such as Chinese/Japanese may have upon complex image recognition, as previously suggested by Kühnen et al. (2001).

2.1 Experiment 1: Object-Scene Composite Recognition

2.1.1 Method

2.1.1.1 Participants

A total of 131 participants took part in the study (61 Western, 57 East Asian and 13 Other; pilot study data indicated that Russian participants did not identify as either Western or Eastern, see Table 2.1). Western participants were students from Lancaster University completing the task for course credit. East Asian and Other participants were recruited from Sunway University using an opportunity sampling method. All students who attended Sunway University required an English language requirement to IELTS minimum band 5.5, defined as a modest English Language User (https://onlineapplication.sunway.edu.my/?m=link&c=entry_requirement). The experimenters comprised English, Mandarin and Malay speakers in order to ensure participants fully comprehended the study. Participants gave informed consent and were reminded they were free to withdraw from the study at any time. Due to data protection issues at Sunway University, age and gender was not recorded for East Asian participants but for Western participants this data was recorded (38 Females, Mean age = 19.28, SE = 0.03). Participants were fully debriefed and informed as to the study’s purpose after completion. Sunway students identifying as Eastern cultures were asked whether they were born/raised in Malaysia. If they were, they would then be asked about their ethnicity. If participants indicated they weren't born in Malaysia they were considered East Asian Other.

Table 2.1. Table showing the total participants in each study by culture and ethnicity

	Ethnicity	Action-Scene Task	Object-Scene Task
Western Cultures	American	6	8
	European	47	39
	Slavic/Eastern European	1	6
	Western Other	8	8
East Asian Cultures	Malay	24	17
	Chinese/Chinese Malay	27	32
	Indian/Indian Malay	7	5
	East Asian Other	9	3
	Other	19	13
	Total	148	131

2.1.1.2 Stimuli

The stimuli consisted of 40 animated objects and 40 images of scenes combined to create a unique object-scene composite. The object-scene composites were taken from an unpublished paper by Urgolites and Wood (unpublished). Each composite consisted of an object performing a 360° rotation for 1 second within one scene (see Figure 2.1) in the centre of the scene. All of the objects had the same duration (1000 ms) and frame rate (30 frames per second), with each object rotating 180° from the starting position at the 15th frame.

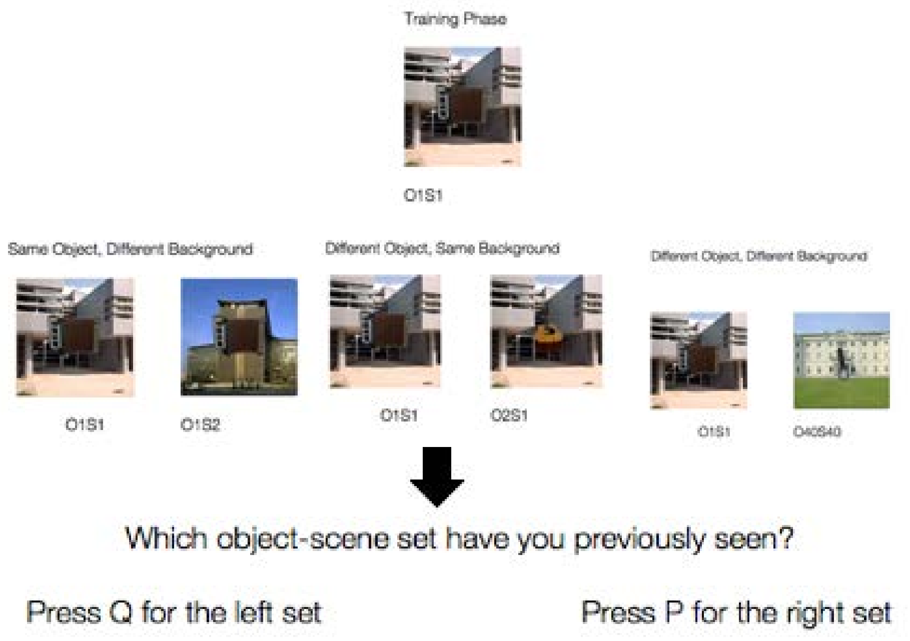

Figure 2.1 Image demonstrating the study and test phase of the object-scene composite recognition task.

2.1.1.3 Procedure

In the study phase participants viewed 40 object-scene composites in a randomised order. Each trial started with a 1000 ms black screen followed by the object-scene composite for 1000 ms, where the object rotated once and after the object-scene composite had been displayed a second 1000 ms black screen was displayed.

In order to ensure participants were maintaining concentration during the study phase after each object-scene composite was displayed, participants performed a repeat-detection task where every 4th novel object-scene composite was repeated at intervals of zero, one, two, three or four trials between the initial presentation and the repeated composite. After each object-scene composite was presented participants were instructed to indicate whether the previous scene had been displayed before with ‘Has this object-scene composite been presented before? Press Z for Old and M for New’ being displayed centrally and ‘Old’ appearing in the left half of the screen and ‘New’ appearing in the right half of the screen, counterbalanced across participants. Participants were able to respond to this without time pressure but were asked to respond quickly and accurately.

The test phase started 2 minutes after the initial training phase. For each trial participants performed a two-alternative forced choice task. Two object-scene composites were presented on a screen: one previously seen ‘old’ composite and one new, foil composite. Participants saw 40 test trials which began with a 1,000 ms black screen, a composite was presented on the left half of the screen for 1000 ms, an interval of 1000 ms with a black screen followed by a second composite presented on the right half of the screen for 1000 ms. After this, a black screen was presented for 1000 ms, then participants were asked which composite had previously been displayed, pressing Q for the left composite and P for the right composite. Both the old composite and the foil composite were only presented once for the full duration of the object’s rotation and were hidden immediately after the rotation had completed. The side in which the old composite was displayed was counterbalanced so it appeared equally across both the left and right sides of the test phase.

Foils within the study were split into two categories, FC-C and FC-NC. In the FC-C category, in Binding Condition (BC) A participants were presented with the old composite whilst the foil composite had the same scene but different object (DFSB). In BC B the old composite was presented with a foil composite with the different scene but same object (SFDB). For the FC-NC category, BC C had the old composite presented with a foil composite with a different scene and different object (DFDB). All backgrounds and foregrounds were taken from stimuli seen in the training task, just in new pairings.

For all tasks participants were given verbal instructions before the experiment started and written instructions were provided on the screen before each section of the experiment. The study was created on Psychopy 1.83.05 (Peirce, 2009).

2.1.2 Results and Discussion

The dataset was initially filtered by proportion of items correctly identified in the training phase so that only results higher than 50% were included in the dataset as any data below that would be less than chance and indicates participants may not have fully understood the instructions. This left 126 participants (55 East Asian, 58 Western, 13 Other), further analysis found that the Other category lead to no significant difference and as such was removed from further analysis leaving 113 participants (55 East Asian, 58 Western). Analysis of ethnicity also led to no significant difference and as such there was no further analysis on this.

Linear mixed effects (LME) modelling was conducted in order to allow us to account for random effects between item and participants. In the analysis the model was initially fitted with a base model of participant number composite to measure random effects, Model AIC = -239.353. We then added the experimental conditions gradually over a series of models. Introducing Culture led to a significant difference compared to the previous model, χ^2 = 6.2288, p = 0.012, Model AIC = -252.945, suggesting that culture had a significant impact on the ability to recognise object-scene composites. Introducing Foreground/Background foils as a factor also increased the model fit, χ^2 = 10.405, p = 0.005, Model AIC = -247.210, suggesting that Foreground/Background foils had a significant influence on recognition. Adding in the interaction between Culture and Foil led to a better model fit but was only borderline significant, compared to the previous model, χ^2 = 5.0834, p = 0.078 (see Table 2.2 for full LME information, Figure 2.2 for visual representation of results).

Table 2.2. Summary of the Linear Mixed Effect Model for the Action-Scene Recognition Task.

Fixed Effects	Estimate	Standard Error	t value	p value
Intercept	0.822	0.048	17.028	$p < 0.001$
Culture	-0.082	0.031	-2.690	$p = 0.007$
Type of Foil	-0.149	0.068	-2.191	$p = 0.029$
Culture * Type of Foil	0.064	0.043	1.483	$p = .139$
	AIC= -234.384	BIC = -230.575	LogLik = -236.384	

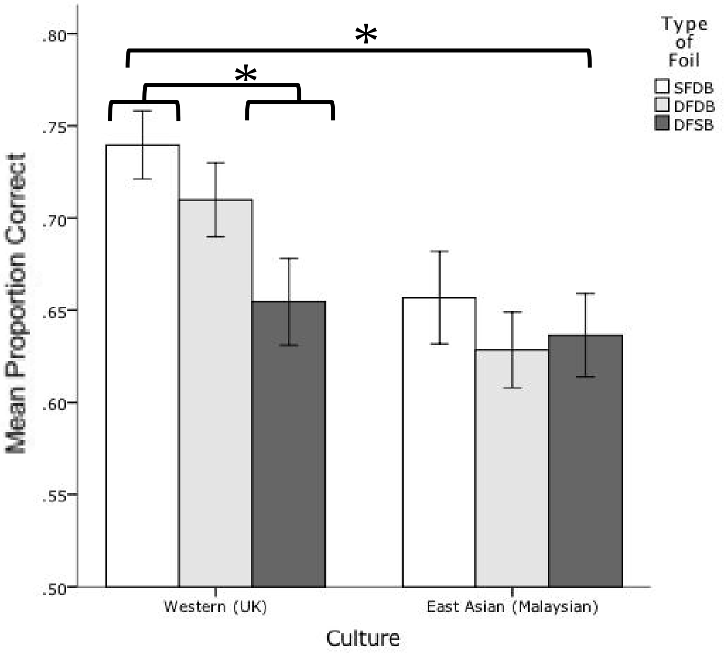

Figure 2.2. Graph showing the average proportion of items correctly identified for each culture. Bars indicate accuracy by type of foil, SFDB- Same Foreground Different Background; DFSB- Different Foreground Same Background; DFDB- Different Foreground, Different Background. Errors Bars represent ± 1 SEM

The result appeared to support our initial hypotheses; holistic processing used by East Asian cultures reduces proportion of items correctly identified of specific object-scene composites compared to Western cultures that employ analytical processing. Although there were differences based on foil type with SFDB significantly more accurate than other foil types, this was not found to interact with culture, suggesting this was an overall effect. However, as previous studies have observed differences based upon stimuli type, with familiarity to stimuli affecting the results (Masuda & Nisbett, 2001, 2006), it was unclear if these results were due to a difference in culture or a difference in familiarity to the object stimuli. In order to control for any cultural differences in familiarity to object stimuli, the following study examined exposure and familiarity to the target objects between East Asian and Western cultures.

2.2 Experiment 2: Cultural Familiarity of Object Stimuli

2.2.1 Method

2.2.1.1 Participants.

A total of 31 participants (15 East Asian, 16 Western) were recruited from Sunway University Psychology club and Lancaster University Psychology Society. Participants were given full information of the study before completing and were free to withdraw from the study at any time.

2.2.1.2 Stimuli.

A total of 40 objects were taken from experiment 1. Objects had the background removed so participants could only focus on the object. Static objects were presented in the centre of the screen with no time restriction.

2.2.1.3 Procedure.

Participants completed this study online and were free to do so without experimenter supervision. Like the previous experiments, before starting participants supplied some cultural/ethnicity information. Participants were given the choice between classifying themselves as Western, East Asian or Other. As this questionnaire was more interested in cultural familiarity rather than ethnicity, no questions were asked about ethnicity. Participants then saw an object and had to indicate whether they had seen the object before (Yes/No) and how familiar the object was on a 6-point Likert Scale, from Extremely Familiar (1) to Not Familiar at all (6).

2.2.2 Results and Discussion

The proportion of familiar objects and average familiarity rating were calculated for each culture (see Table 2.3). A between-subjects ANOVA with Culture as the independent variable and mean proportion recognised and average familiarity rating as dependent variables. There was no significant difference between cultures in proportion recognised, $F < 1$, or average familiarity ratings, $F < 1$. The result suggested that there was no difference in object exposure based upon culture, thus the results of experiment 1 were legitimate and that there was a significant cultural difference in specific object-scene composite recognition.

Table 2.3. Table showing mean proportion of objects recognised and average familiarity rating by culture.

	Mean proportion of objects recognised	Average Familiarity Rating
East Asian	0.975 (0.025)	1.598 (0.058)
Western	0.981 (0.006)	1.583 (0.059)

2.3 Experiment 3 Action-Scene Composite Recognition

In the previous study it was demonstrated that Western cultures were significantly more accurate than East Asian cultures in proportion of items correctly identified of specific object-scene composites. Within the current experiment, we sought to extend this result by changing the stimuli to action-scene composites, as used by Urgolites & Wood (2013b). Within their study, they observed that proportion of items correctly identified was only just above chance levels, averaging 56%. As the study used an American sample, it was unclear if the accuracy level was due to the type of visual processing or due to the complexity of the stimuli. Our first hypothesis was Western participants would replicate the results of Urgolites & Wood (2013b); proportion of items correctly identified would be significantly above chance, albeit only slightly. Our second hypothesis was that based upon the results of experiment 1a, there would be no significant difference between Western and East Asian cultures for specific action-scene composite recognition.

2.3.1 Method

2.3.1.1 Participants.

Before the experiment started participants indicated some cultural/ethnicity information. Participants were given the choice between classifying themselves as Western, East Asian, or Other (pilot study data indicated that Russian participants did not identify as either Western or East Asian). For those that Identified as Western, they were then given the option to identify themselves as American, European, Slavic, or Western Other. Those identifying as Eastern were given the option as identifying as Malay, Chinese/Chinese Malay, Indian/Indian Malay, or East Asian Other.

A total of 148 participants took part in the study (62 Western, 67 East Asian and 19 Other, see Table 2.4). Western participants were students from Lancaster University who were set to conduct the research at Sunway University and undergraduate psychology students completing the task for a course credit. Participants completed the study before travelling and had no prior knowledge as to what the study consisted of so as to prevent demand characteristics but were fully informed as to the study’s purpose both after completing the study and before administering the test at Sunway University. East Asian and Other participants were recruited from Sunway University using an opportunity sampling method. All students who attend Sunway University require an English language requirement to IELTS minimum band 5.5, defined as a modest English Language User fully detailed on the website. To mitigate any confound of lack of comprehension within the research team, two research assistants were fluent in Mandarin and one in Malay speakers in order to ensure participants fully comprehended the instructions. Participants gave informed consent and were reminded they were free to withdraw from the study at any time. Due to data protection issues at Sunway University, age and gender was not recorded but this information were obtained from the Western sample, (33 Females, Mean age = 18.97, SE = 0.14), however research from a secondary study has indicated no gender or age differences (Shaw, Monaghan, & Urgolites, in draft). Sunway students identifying as East Asian cultures were asked whether they were born/raised in Malaysia. If they were, they were then asked about their ethnicity. If they indicated they weren't born in Malaysia, they were considered East Asian Other. Participants were fully debriefed and informed as to the study's purpose after completing the study.

Table 2.4. Table showing total participants in each study by culture and ethnicity.

	Culture	Action-Scene Task	Object-Scene Task
	American	6	8
Western Cultures	European	47	39
	Slavic/Eastern European	1	6
	Western Other	8	8
East Asian Cultures	Malay	24	17
	Chinese/Chinese Malay	27	32
	Indian/Indian Malay	7	5
	East Asian Other	9	3
	Other	19	13
	Total	148	131

2.3.1.2 Stimuli.

The stimuli consisted of 40 animated actions and 40 images of scenes combined to create an action/scene composite. The actions were taken from a previous paper that had examined fidelity of actions in VLTM by Urgolites and Wood (2013a) whilst the scenes were taken from a study examining the fidelity of scene representations in VLTM by Konkle et al. (2010). The combined composites were taken from a previous study by Urgolites and Wood (2013b). Each composite consisted of an action being performed for 1000 ms within one scene (see Figure 2.3). The actions appeared in the centre of the scene. All of the actions had the same duration (1000 ms) and frame rate (30 frames per second) with each action reaching its maximum deviation from the neutral standing position at the 15th frame. The action stimuli included jumps, turns, bends and crouches. The stimuli set included mountains, beaches, oceans, forests and cities. The study was created on Psychopy 1.83.05 (Peirce, 2009)

2.3.1.3 Procedure.

Procedure for this study was the same as the experiment 1 (See figure 2.3).

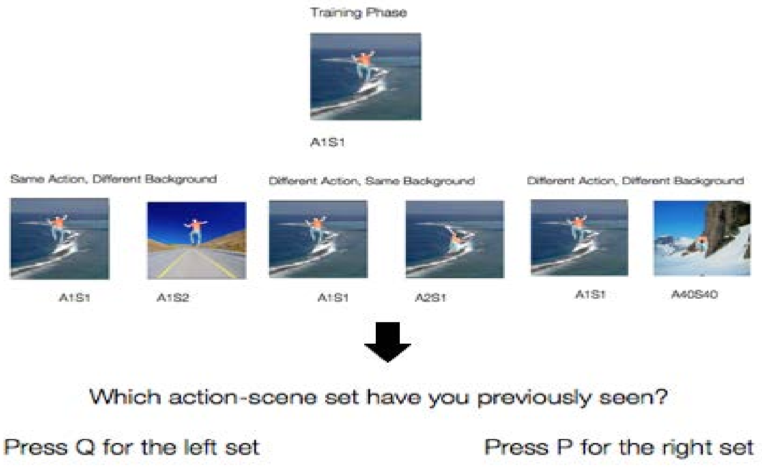

Figure 2.3 Image demonstrating the study and test phase of the action-scene composite recognition task.

2.3.2 Results and Discussion The dataset was initially filtered by proportion of items correctly identified in the training phase so that only results higher than 50% were included in the dataset as any data below that would be less than chance and indicates participants may not have fully understood the instructions. This left 145 participants, (65 East Asian, 61 western, 19 other, accuracy M = 97.6%, SE = 0.05). Further analysis found that the Other category lead to no significant difference and as such was removed from further analysis leading 126 participants to be analysed. Analysis of ethnicity also led to no significant difference and as such there was no further analysis.

Linear mixed effects (LME) modelling was conducted in order to allow us to account for random effects between item and participants. In the analysis, we used a series of models

Model 1. A model with just random effects (Participant ID and action-scene pairing)

Model 2. A model introducing Culture as a factor

Model 3. A model introducing Culture and Foils as factors

Model 4. A model introducing Culture and Foils as factors along with the corresponding interaction.

We found that each increment in complexity did not differ significantly from the previous model, comparing Model 1 and 2 $\chi^2 = 1.0014$, $p = 0.317$; comparing Model 2 and 3, $\chi^2 = 1.918$, $p = 0.5895$, comparing Models 3 and 4, $\chi^2 = 2.7883$, $p = 0.248$. The results suggested that culture and foil did not significantly affect proportion of items correctly identified of action-scene composites. Although different from the results of experiment 1, the result was consistent with previous literature on specific recognition of action-scene composites (Urgolites & Wood, 2013b), suggesting that the reduced proportion of items correctly identified for action-scene composites was not unique to Western culture, but is generally more difficult than recognition of object-scene composites.

Table 2.5. Summary of the Linear Mixed Effect Model for the Action-Scene Recognition Task.

Fixed Effects	Estimate	Standard Error	t value	p value
Intercept	0.569	0.016	34.303	$p < 0.001$
Culture	0.006	0.023	- 1.915	$p = 0.056$
Type of Foil	-0.035	0.023	-1.503	$p = 0.133$
Culture * Type of Foil	0.042	0.032	1.299	$p = 0.194$
	AIC= -437.016	BIC = -433.097	LogLik = -439.016	

Table 2.6. Table showing the average proportion of items correctly recognised for Western and East Asian cultures split by Task and foil type. SE in parentheses.

	Action-Scene Task			Object Scene Task		
Culture	SFDB	DFDB	DFSB	SFDB	DFDB	DFSB
Western	0.536	0.570	0.534	0.740	0.710	0.655
(UK)	(0.019)	(0.018)	(0.015)	(0.018)	(0.020)	(0.024)
East Asian	0.542	0.525	0.533	0.657	0.628	0.636
(Malaysian)	(0.017)	(0.015)	(0.014)	(0.025)	(0.021)	(0.023)

Mean Proportion of Composites Recognised

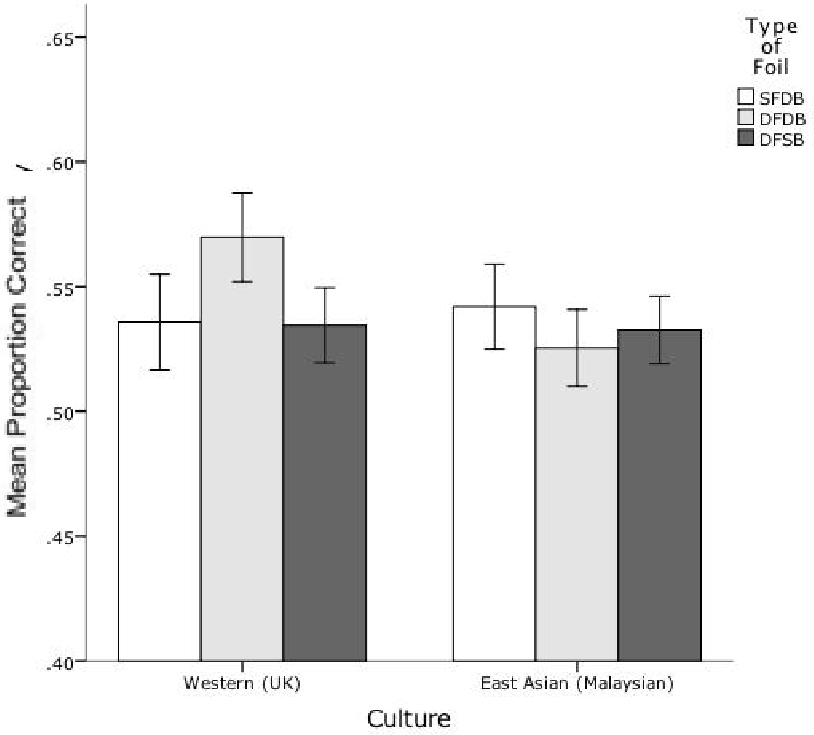

Figure 2.5. Graph showing the average accuracy for each culture. Bars indicate accuracy by type of foil, SFDB- Same Foreground Different Background; DFSB- Different Foreground Same Background; DFDB- Different Foreground, Different Background. Errors Bars are ± 1SEM.

3. General Discussion

Within the current study we sought to extend the previous literature that has demonstrated cultural differences between East Asian and Western cultures in separate item (Chua et al., 2005; Masuda & Nisbett, 2001), and context (Millar et al., 2013) recognition to see if this would also apply to specific item-context composites. In Experiment 1, there was a significant difference in specific object-scene composite recognition based on culture; UK participants were significantly more accurate than Malaysian participants. Experiment 2 revealed that this difference was not due to cultural differences in object familiarity. When extended to action-scene composite recognition, the result of Experiment 3 replicated the results previously observed by Urgolites & Wood (2013b) that action-scene composite recognition is above chance, albeit only slightly, in a UK sample, but also demonstrated the same effect in a Malaysian sample, suggesting that culture is not a significant factor in difficulties associated with action-scene composite recognition.

The question then becomes why are Western cultures more accurate in recognising specific object-scene composites compared to East Asian cultures, and why this effect seems specific to object-scene and not action-scene? The latter may be more easily explained; One explanation is the differences in complexity of the foreground stimuli and processing it in the time frame given. Within all experiments reported, participants saw the action-scene/object-scene pairs for 1000 ms. Whilst object recognition is fast, with brain responses associated with visual discrimination of objects occurring around 150ms (Allison, Puce, Spencer, & McCarthy, 1999; Thorpe, Fize, & Marlot, 1996), action recognition within the current study is not possible until 500ms (where the action reaches maximum deviation from the neutral standing position, making what action it is clearest), leaving less time to process the background information, thereby potentially reducing the fidelity any bound representation. As participants only had 1000 ms to process all this information, it could be that any potential cultural differences in the action-scene task did not have enough time to manifest. In Urgolites & Wood’s (2013b) study there was a small but significant increase in accuracy when the action was repeated three times against the same background. While this was not conducted here, it would be interesting to see if any cultural effects could be replicated if there was more exposure to the focal foreground item. In addition to this, differences in encoding requirements could be linked to this difference; object-scene composites only require encoding over space, whereas for actions, long-term memory must encode dynamic information distributed over space and time, thus any bound representation may be more fragile.

For the former, it may be that the cultural differences in visual processing also lead to cultural differences in visual binding. One theory suggested by Chalfonte and Johnson (1996) suggests there are at least two ways that feature binding may be expressed. Features may be independently represented but associated or features may form a blended representation, distinct from processing the two features separately (Chalfonte & Johnson, 1996; Graf & Schacter, 1989). When applied to the results of Experiment 1, it appears that Western participants employ this independent but associated representation; analytical processing ensures high-fidelity representations of the visual features are encoded and the association between the elements is maintained, consistent with existing literature (Millar et al., 2013; Urgolites & Wood, 2013b). In contrast, East Asian participants that engage in holistic processing, encoding the entire visual scene as one contextualized representation, result in a blended representation with reduced visual fidelity of each feature, making it difficult to correctly recognize specific composites. This explanation would also appear consistent with the previous literature as to why East Asian participants respond quicker than Western participants but are also typically less accurate in recognition tasks (Masuda & Nisbett, 2001); by having a blended representation of the entire visual scene it allows judgement based on familiarity but the reduced fidelity makes the judgement more prone to errors. In contrast, having independent but associated high-fidelity representations would allow a more accurate recognition judgement but at the expense of a longer reaction time, as seen in Masuda and Nisbett (2001).

Alternatively, the observed cultural difference may be due to issues regarding visual incongruity. Memory for scene items has previously been demonstrated to be diminished when object-background pairs are semantically incongruent due to required interactive processing of object and background

(Davenport & Potter, 2004). Jenkins et al. (2010) demonstrated in an fMRI study that Chinese participants demonstrated a heightened response to semantically incongruent scenes compared to American participants. The style of the composites, with the object rotating above the visual scene, it may have facilitated the object-based analysis favoured by Western cultures (Jenkins et al., 2010). Further studies could attempt to address this by measuring recognition of specific item-background photographs.

A second consideration for future studies could be extending the East Asian sample to multiple countries. The current study, for design reasons, was primarily focused upon a Malaysian sample. As Malay is a latin-based language, it was chosen in order to account for any potential confounds a pictographic language may have in visual memory, with previous studies highlighting this importance (Kühnen et al., 2001). As a result, it may be that this sample is not wholly representative of the larger East Asian culture, such as Chinese, Japanese, or Korean cultures that use a pictographic language. As such, further studies may want to focus on these cultures in order to see if the effect can be replicated. It may be the case that cultures with a pictographic language may be able to process the intricate details of an item-context scene better, due to having to identify the various specific differences between language characters (Kühnen et al., 2001).

In summary, within the current study we have empirically demonstrated that previously suggested cultural differences in visual processing can extend to feature binding. By processing scenes analytically, Western cultures are able to store high-fidelity representations of visual features and maintain an association between them. In contrast, holistic processing creates a blended representation, a reduced fidelity representation of the whole visual image that allows general familiarity, but reduced specific recognition. This difference appears to be limited to object-scene composites with no cultural difference observed for action-scene composites, possibly due to the increased complexity of the visual image.

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Chapter 3. The impact of Sleep on relational binding of actions, objects, and scenes in visual long-term memory

In the previous chapter we sought to expand on the previous literature that has demonstrated that relational binding in the VLTM is particularly difficult. Within the study it was demonstrated that while the object-scene composite recognition was significantly affected by culture, with Western participants more accurate than East Asian participants, performance on the action-scene composite recognition task was consistent across both cultures, averaging close to chance levels.

With this established, the thesis moved onto one of the main aims, to understand the role that sleep may have on consolidation of these action-scene/object scene composites. Previous literature has demonstrated that sleep can have a consolidating role on associative memory, but most of this is in the form of associative pairs, with one item cueing another. In order to explore high-fidelity representations, the following study uses the same methodology as the Culture study, but utilises a sleep/wake delay to account for interference.

Draft prepared for submission to Psychological Science

Abstract

Previous research has demonstrated that visual long-term memory has a large and detailed storage capacity for scenes, objects, and actions. However, when required to recall which action had occurred within which scene, performance drops significantly suggesting there is a dissociation between memories for actions and scenes. Sleep has been shown to have a strong impact on declarative memory, but can sleep affect joint recognition? Across three experiments participants viewed action-scene or object scene composites and were assigned to either an experimental condition with a 12-hour delay consisting of sleep (9pm-9am) or wake (9am-9pm) or a control group (9am or 9pm) with a two minute delay. Participants then viewed the composites for 1000-3000ms each. In the test phase, participants completed an alternative forced choice task whereby they were shown an original set and a new, unseen set and had to indicate which one they had previously seen. For action-scene composites, there was no significant difference between groups with sleep (49.5%) and wake (50.6%) performing around chance, which did not differ significantly from two control groups. For object-scene composites there was a significant difference between the sleep group (67.3%) and the wake group (59.7%). Those in control groups were the most accurate. The findings demonstrate that for object-scene composites, while immediate testing is most accurate, sleep appears to preserve and consolidate the memories when compared to a wake delay but this was not apparent for action-scene composites. This result is discussed in relation to the existing sleep literature

Keywords: Sleep, Visual Long-Term Memory, Binding Memory, Item-Context Recognition

Highlights:

- Object-scene composite recognition was significantly higher than action-scene composite recognition
- Sleep had a beneficial impact on consolidation of object-scene composites, but not action-scene composites

1. Introduction

Within the literature on visual long-term memory (VLTM), it has been demonstrated that humans have a remarkable capacity to store item representations (Standing, 1973; Hollingworth, 2004). However, it is a mischaracterisation to judge it based on the number of items stored. These representations are not just item representations of each individual item, rather these representations are highly-structured, allowing for multiple levels of representations ranging from individual item level (e.g., what your car looks like) through to higher-level conceptual representations (e.g., what makes a car; Konkle, Brady, Alvarez, & Oliva, 2010a).

Studies investigating specifically memory capacity have demonstrated a remarkable allowance. In a seminal paper, Standing (1973) observed that participants were highly accurate in recognition of previously seen images, even when presented with over 10 000 images participants could recognise approximately 87% of them, leading to suggestions that VLTM is effectively unlimited and only restricted by how visually distinctive an item is compared to similar items.

Yet distinctiveness does not seem to be a limiting factor. Studies have demonstrated that item representations are constructed in a high-fidelity manner. For example, Hollingworth (2004) noted that participants were able to maintain sufficient detail to distinguish between items within the same categories or even different viewpoints, with above chance recognition observed across 400 objects, even after a 24h delay (Hollingworth, 2005). In an effort to replicate and extend the work of Standing (1973), Brady, Konkle, Alvarez, and Oliva (2008) presented participants with over 2500 categorically distinct items and then asked them to complete a two-alternative-forced-choice task (2AFC) varying the relationship between the target item and the foil item, so that it was a novel category item, requiring memory for only the semantic category (e.g., var v mobile phone), a novel, exemplar-level item, requiring a level of fidelity that could not be utilised from semantic level (e.g., a limousine v a sedan car), or state-level item, the exact same item, just in a different state (e.g., a sedan car v the same car with the door open).

Amazingly, performance across all conditions was close to ceiling, with even the state-foil condition recognition accuracy averaging 87%, suggesting that humans can store high-fidelity representations of recently learned items. Furthermore, this effect is not limited to objects, with recent literature demonstrating similar performance levels for both scenes (Konkle, Brady, Alvarez, & Oliva, 2010a, 2010b), and actions (Urgolites & Wood, 2013a).

One of the suggestions for how humans can store high-fidelity representations to this level is through what Konkle et al. (2010b) term a “conceptual hook”. The idea is built upon consolidation models of memory, such as the Complementary Learning Systems (CLS) model (Squire, 1992; McClelland et al., 1995) or Multiple Trace Theory (MMT, Nadel et al., 2000) that suggest interaction between hippocampal and neocortical representations leads to consolidation of representations. Although the literature is too vast to describe within this paper, to summarise representations are initially located within the hippocampus and through repeated activation they become interleaved within a neocortical semantic network that contains pre-existing conceptual knowledge (McClelland et al., 1995) until the hippocampal representation is no longer required and subsequent retrieval can occur from neocortical sites. To create this conceptual knowledge, the memory often undergoes a qualitative reorganisation, with commonalities between episodic representations being extracted to form the conceptual representation, a process often termed semanticisation (McClelland et al., 1995). The resulting neocortical representation is not a direct copy of the episodic representation, but rather a representation that can be used to generalise to similar items, similar to schema theory (Bartlett, 1932; Brewer &

Nakamura, 1984; Norman, 1972; Rummelhart, 1980; Spiro, 1977). Within the conceptual hook model by Konkle et al. (2010b), there is a form of item prototype that can act as a prompt for both encoding as retrieval. For example, the conceptual hook for a car may be a motor vehicle with four wheels and at least one door. Moreover, each item prototype can be linked to multiple exemplars and the variation within this is what affects recognition. For the above example of a car there is a wide variation is possible category-based exemplars, ranging from mini coopers through to limousines. In contrast, for an item like a microwave, there is much less variance and as such, more prone to interference.

The conceptual representation is not just limited to individual items but by its nature of being generalisable can also associate representations together. Several studies have also looked at the relationships between objects and other objects as well as between objects and the surrounding scene (see Luck & Hollingworth, 2008), often termed schemata (Biederman et al., 1982; Hock, Romanski, Galie, & Williams, 1978) or context frames (Bar & Ullman, 1996; Bar, 2004). In having this association, even presentation of a single item from schemata can trigger associative expectation of related items (Bar et al., 2006), with multiple studies demonstrating that when items are presented in a context consistent with expectations accuracy can increase or occur faster (Davenport & Potter, 2004). For example, Hollingworth (2006) observed that participants who studied a scene with multiple objects in it performed significantly better at an object recognition task when the object was presented within the presented scene, with a similar effect observed in spatial positions of objects (Hollingworth, 2007). Although these studies were presented at a relatively short timeframe, the results mirror that of the encoding-specificity principle (Tulving & Thomson, 1973) which suggests that the better the match between encoding and retrieval, the better the performance.

Although conceptual knowledge of visual representations has been demonstrated to led to expedited encoding, it can also lead to retrieval errors/ errors of commission, whereby associated items are falsely recalled as being part of the representation. For example, after studying items in a series of scenes (e.g., golf course), participants are more likely to falsely recognise a schematic-consistent item (e.g., a golf club) than a schematic-irrelevant item (e.g., a fridge; Miller & Gazzaniga, 1998). Moreover, Lew and Howe (2016) demonstrated that the influence of visual schema can influence location of objects within a scene, but schema irrelevant items (e.g., a toilet brush in a kitchen scene) are recognised to a high level due to the uniqueness. These errors of commission typically come about through the expectation of the scene, although you are unsure if the item was there, given the expectation of it due to the schema it is more likely that it was than wasn't, akin to the false memory generation as seen in the DRM paradigm (Deese, 1959; Roediger & McDermott, 1995).

Despite there being a wide literature on associations formed in the VLTM, few studies have examined recognition of specific composite pairs, i.e., making judgements about whether a specific item-item pair has been previously seen when presented in a 2AFC task. Although studies have demonstrated a role of context in VLTM as outlined in the previous paragraph, most of these are formed through cued associative pairs, where participants are presented one half of the pair and have to retrieve the associated item, meanwhile recognition of unrelated pairs is relatively unresearched. One study, Urgolites & Wood (2013b) examined the ability of the VLTM to associate specific actions and scenes as a form of composite pair. In their study participants viewed 40 unique action-scene composites (e.g., a1s1, a2s2) and at retrieval were presented with a 2AFC task containing the target composite and a foil item containing a novel composite but containing a previously seen element (e.g., for the above example, the foil may be a1s2 or a2s1). It was observed that overall performance was only just significantly above chance (59%), although performance on recognition of just the action or scene separately close to previously reported levels (Konkle et al., 2010a, Urgolites & Wood, 2013a). Urgolites and Wood (2013b) suggested that the issue was not one of encoding or retrieving individual actions or scenes, but one of relational binding, although it is unclear if this was an issue of binding at encoding or retrieval. One suggestion by Urgolites and Wood (2013b) was that actions and scenes are stored separately within the VLTM. There is some neurophysiological evidence for this dissociation with studies demonstrating at least four dissociated cortical pathways within visual cognition (reviewed by Kravitz et al., 2011). To summarise, the ventral pathway is thought to support object recognition while the dorsal pathway contributes to the ability to track movement and location of objects projected to the prefrontal cortex, scene-based recognition for spatial navigation projected to the medial temporal lobe, and visually guided actions projected to the premotor cortex (Kravitz et al., 2011). By nature of this disparate processing areas and the requirement of processing at both a temporal and spatial level, binding of actions and scenes in the hippocampus may have been too difficult. At the time of writing this, although studies have looked at the relationship between object and scene-as-a-context in retrieval, none have looked at recognition of the specific object-scene pairing in a 2AFC task similar to Urgolites & Wood (2013b).

Within the current study one of our aims was to see if there was any difference between recognition for object-scene composites and action-scene composites. If difficulty associated with relational binding at encoding or retrieval is unique to action-scene composites, there should be a significant difference observed between action-scene and object-scene composites.

The second aim of this paper was to determine if sleep may have an effect on this form of relational binding. Modern theories of consolidation (e.g., McClelland et al., 1995; Winocur et al., 2010) emphasise how hippocampal reactivity during sleep is influential for memory consolidation (see Diekelmann & Born, 2010; Rasch & Born, 2013). Across a range of studies, sleep has been demonstrated to have a beneficial role in learned associative pairs compared to a period of wakefulness. This effect was demonstrated in cued associative tasks that use a range of stimuli including related- and unrelated- word pairs (Gais & Born, 2004), item-context pairs (van der Helm et al., 2011), and face-location pairs (Ruch et al., 2012). One of the suggestions for this beneficial effect of sleep on consolidation is the semanticisation that can occur during sleep and that facilitates extraction of regularities and the integration of information into unified representations. For example, Wagner et al. (2004) was the first to demonstrate that sleep can aid consolidation of concepts by noting that a period of sleep facilitated participants insight into a hidden rule in a number reduction task. Subsequent studies have further extended the importance of sleep in abstraction of common themes and proto-rules (Durrant & Lewis, 2009; Gomez et al., 2006; Fischer et al., 2006; Nadel et al., 2012; Nere et al., 2013; Sio, Monaghan, & Ormerod, 2013), although abstraction during sleep can lead to generation of false memories (Monaghan, Shaw, Ashworth-Lord, & Newbury, 2016; Pardilla-Delgado & Payne, 2017; Payne et al., 2009; Shaw & Monaghan, 2017).

Our third aim was to examine the role of sleep in composite recognition. As sleep has been demonstrated to have a beneficial effect on learning associations, it is unclear what role it may have on the action-scene and object-scene composites. It may be that sleep has a compensatory effect on relational binding of action-scenes, acting to consolidate the poorly bound association to above chance levels. Alternatively, if sleep does preferentially bind representations that are already strongly bound, it may be that object-scene composites experience a greater benefit from sleep.

2.1 Experiment 1a: The role of sleep in action-scene Relational Binding: Experimental Groups

2.1.1 Method

2.1.1.1 Participants

A total of 40 undergraduate participants (28 females, 12 males, mean age =19.26, SEM= .03) with normal or corrected to normal vision initially signed up to the study agreeing to be tested on two sessions that were set twelve hours apart. Then the experimenter assigned the participants to their specific timeslot in order to avoid any potential time preferences in the participants. Sample size was set to 20 in each group based upon previous sleep studies (Rasch & Born, 2013). Participants were asked to maintain a normal sleep schedule for the two days prior to testing, to sleep for at least 6h for the night preceding the study, and to refrain from drinking alcohol and caffeine for at least 12h prior to the start of the study. Participants reported mean bed times of 10:56pm, wake times of 8:14am and average sleep times of 7h 32m.

Participants were either given course credit or were paid £7 for participating upon completion of the study after the second session. Participants gave informed consent and were reminded they were free to withdraw from the study at any time without incurring any penalty.

2.1.1.2 Stimuli

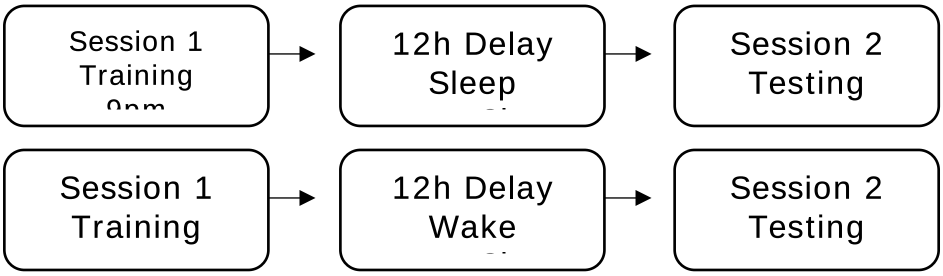
The stimuli consisted of 40 animated actions and 40 images of landscape scenes combined to create 40 action/scene composites for the learning phase. The actions were taken from a previous paper that had examined fidelity of actions in VLTM by Urgolites and Wood (2013a), whilst the scenes were taken from a study examining the fidelity of scene representations in VLTM by Konkle et al. (2010). The combined composites were taken from a previous study by Urgolites and Wood (2013b). Each composite consisted of an action being performed for 1000 ms within one scene (see Figure 3.1). The actions appeared in the centre of the scene. All of the actions had the same duration (1,000 ms) and frame rate (30 frames per second), with each action reaching its maximum deviation from the neutral standing position at the 15th frame. The action stimuli included jumps, turns, bends and crouches. The scene stimuli included mountains, beaches, oceans, forests and cities. The study was programmed on Psychopy 1.83.05 (Peirce, 2009). Participants completed the Stanford sleepiness scale and completed a questionnaire about their sleep habits and any caffeine/alcohol intake in the last 12h.

For the test, three different types of foil stimuli were created. Foils either had a different foreground action but the same background scene (DFSB) as the target action/scene composite, or the same foreground action but a different background scene (SFDB), or a different foreground action and different background scene (DFDB). All foil composites were created from actions and scenes that were already seen in the study and across all conditions the 40 foils were split by 13, 13, and 14 presented in random order.

2.1.1.3 Procedure

The procedure for the study closely followed that of Urgolites and Wood (2013b), except with the introduction of sleep as an experimental manipulation. The experiment consisted of a study phase and a test phase spaced 12h apart, with the two experimental groups being wake (study phase at 9am, test phase at 9pm) or sleep (study phase at 9pm, test phase at 9am the following day, see Figure 3.1). In the study phase participants viewed 40 action-scene composites. Each trial started with a 1000 ms black screen followed by the action-scene composite for 1000 ms where the action was performed once. Then, a second 1000 ms blank screen was displayed. To ensure participants were maintaining concentration during the study phase, after the post-composite blank screen was displayed participants had to respond whether they had seen the scene before, by pressing the Z key or M key on a keyboard for yes or no judgments, respectively counterbalanced across participants. Every 4th action-scene composite was repeated at intervals of zero, one, two, three or four trials between the initial presentation and the repeated trial in order to measure whether participants were paying attention to the task. Participants responded without time pressure but were instructed to respond as quickly and accurately as possible. After the participant responded, the blank screen commencing the next trial appeared. In the wake condition participants were instructed to stay awake during the next 12h and refrain from any form of sleep. In the sleep condition participants were instructed to go to bed and sleep.

The test session began approximately 12h after the test phase. Both groups of participants completed the Stanford Sleepiness scale and participants in the sleep condition also completed a sleep questionnaire detailing how much sleep they had the previous night and caffeine intake. Then participants conducted the memory test, which was a two-alternative forced choice test. Two action-scene composites were presented on a screen: one previously seen and one new foil. Participants saw 40 test trials which began with a 1000 ms black screen, then an action-scene composite appeared on the left half of the screen for 1000 ms, followed by a 1000 ms black screen, and then a second action-scene composite appeared on the right half of the screen for 1000 ms. A black screen was presented for 1000 ms, and then participants were asked which composite had previously been displayed, pressing the Q key on a keyboard for the left composite or the P key for the right composite. The side of the screen on which the old and foil composites appeared were balanced. Although amount of each foil was varied as a counterbalance, across all conditions the 40 foils were split by 13, 13, 14 presented in random order.



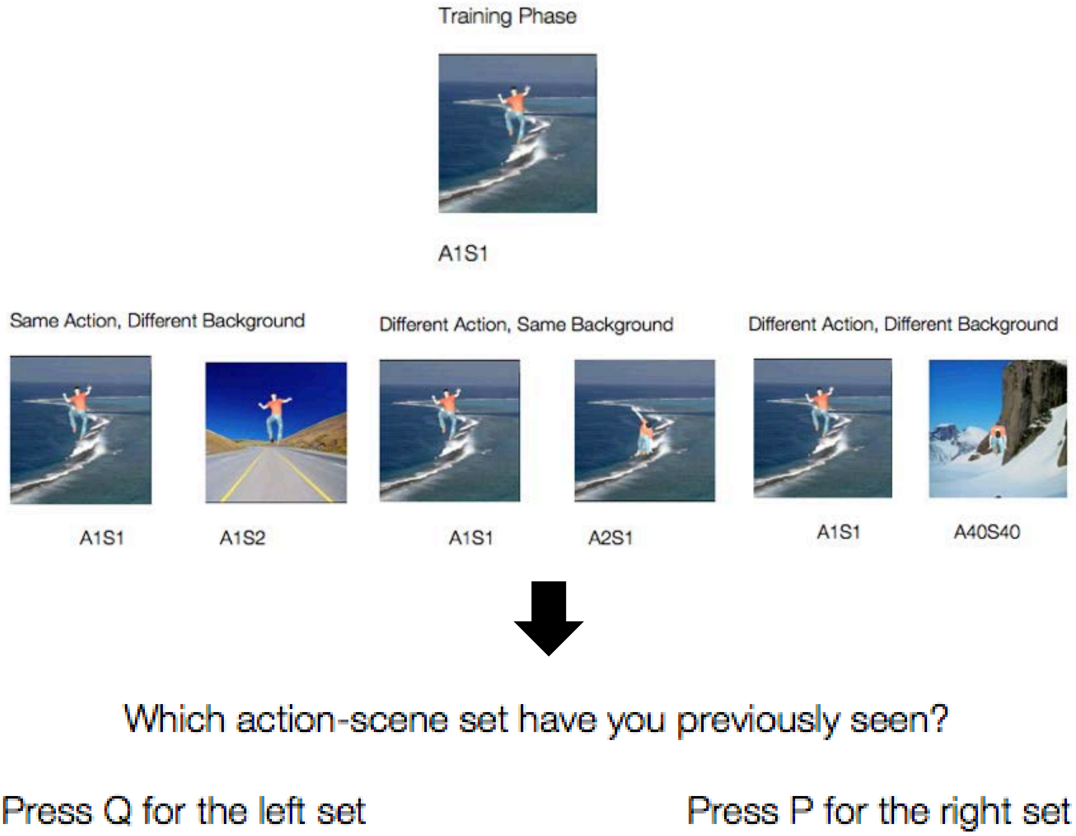


Figure 3.1 Image demonstrating the study paradigm study and test phase of the action-scene composite recognition task.

2.1.2 Results

A 3 (Foil Type) x 2 (Group) ANOVA was conducted on accuracy of recognition. For Group there was no significant difference in accuracy between Sleep (0.511) and Wake (0.509), $F < 1$, $p =$ ns suggesting that sleep had no beneficial impact on the binding of action-scene composite. The observed accuracy levels did also not differ from chance performance, sleep group t(19) 0.636, *p* = ns, wake group t(19) 0.424, *p* = ns. For Foil Type there was no significant difference between SFDB (M = 0.517), DFSB (M = 0.532) or DFDB (M = 0.482), F(2, 38) = 1.377, p = 0.253. There was also no significant interaction between group and foil type, *F* < 1, *p* = ns. As there was a delay between the display of the first composite and the time a participant could respond, reaction times were not included in any further analysis.

2.2 Experiment 1b Sleep’s role in action-scene Relational Binding: Control Groups

The result of Experiment 1a demonstrated that sleep had no beneficial effect on consolidation of action-scene composite recognition, with both the sleep and wake group reporting proportion of items correctly recognised at chance levels after the 12h delay, suggesting that the result was due to the length of the delay. In order to examine this further, the following study replicated that of Urgolites and Wood (2013b) by presenting the recognition task 1 minute after the training task. The testing time of participants was varied between the morning and the evening, so that the potential contribution of the delay to memory binding could be tested at these different times of day.

2.2.1 Method

2.2.1.1 Participants

A total of 40 undergraduate participants (28 females, 12 males, mean age =19.48, SEM= 0.07) with normal or corrected to normal vision and who had not taken part in Experiment 1a were assigned to groups as outlined in Experiment 1a. Participants were asked to maintain a normal sleep schedule for the two days prior to testing, to sleep for at least 6h for the night preceding the study, and refrain from drinking alcohol and caffeine for at least 12h prior to the start of the study. Participants reported mean bed times of 12.36am, wake times of 08.43am, mean sleep duration of 8h 7m. Participants were given course credit or £3.50. Participants gave informed consent and were reminded they were free to withdraw from the study at any time without incurring penalty.

2.2.1.2 Stimuli

Stimuli used for the study were the same as those used in Experiment 1a.

2.2.1.3 Procedure

Participants were randomly assigned to either a morning (9am) or evening (9pm) condition. First, participants completed the Stanford sleepiness scale and completed a questionnaire about their sleep habits and any caffeine/alcohol intake in the last 12 hours. Participants then completed the study phase of the action-scene composites. After completing the study phase, there was a 1 minute pause, after which participants completed the test phase in exactly the same way as in Experiment 1a.

2.2.2 Results

A 3 (Foil Type) x 2 (Group) ANOVA was conducted on proportion of items correctly recognised. For Group there was no significant difference between Morning (M = 0.552, SE = 0.018) and Evening (M = 0.549, SE = 0.018), F < 1, *p* = ns. The observed accuracy levels did significantly differ from chance performance, evening group t(19) 3.056, *p* = 0.002, evening group t(19) 2.841, *p* = 0.005. There was also no significant difference based upon Foil Type, F(2, 38) = 1.402, *p* = 0.246, and no significant interaction between group and foil, F < 1, *p* = ns. When compared to the groups in Experiment 1a, there was a significant difference of delay condition (immediate versus 12 hour delay), F(2, 78) = 5.283, *p* = 0.022, with the Experiment 1b immediate recognition groups significantly more accurate (M = 0.551, SE = 0.012) than the Experiment 1a delayed recognition groups (M = 0.510, SE = 0.012; see Figure 3.2 for comparison across groups).

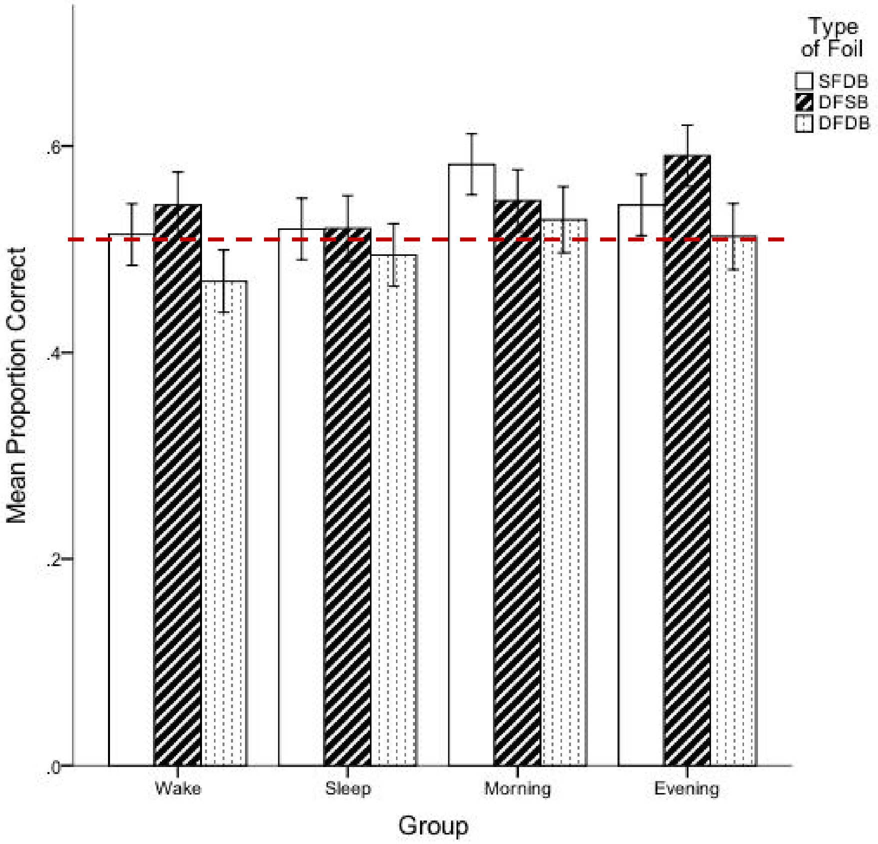


Figure 3.2. Graph showing the average accuracy for each group. Bars indicate mean proportion correct by Foil Type, SFDB- Same Foreground Different Background; DFSB- Different Foreground Same Background; DFDB- Different Foreground, Different Background. Errors Bars are ± 1SEM.

2.3. Experiment 2: Sleep’s role in action-scene Relational Binding: Repeated Viewing

In Experiment 1a it was observed that there was no significant effect of sleep on the consolidation of action-scene composites, with both the sleep and wake group reporting similar proportion of items correctly recognised after a 12h delay, suggesting a time delay effect. Urgolites and Wood (2013b) noted in their study that if the action was repeated three times then proportion of items correctly recognised increased slightly, so Experiment 2 presented repeated stimuli and determined whether a sleep effect could then be observed on action-scene binding memory after a 12 hour delay.

2.3.1 Method

2.3.1.1 Participants

17 undergraduate participants (9 female, mean age = 18.76, SEM = 0.09) with normal or corrected to normal vision were assigned to wake or sleep groups as outlined in Experiment 1a. Participants were asked to maintain a normal sleep schedule for the two days prior to testing and were asked to sleep for at least 6h for the night preceding the study and refrain from drinking alcohol and caffeine for at least 12h prior to the start of the study. Participants reported mean bed times of 12:12am wake times of 8:14am.

Participants were given course credit upon completion of the study after the second session. Participants gave informed consent and were reminded they were free to withdraw from the study at any time without incurring penalty.

2.3.1.2 Stimuli

Action-scene composites used in the current task were the same as those used in Experiment 1a/1b with the exception that the action was performed three times. The figure started from a neutral position and reached maximum deviation from the neutral position at 500ms, and returning to the neutral position at 1000ms. This was looped 3 times so that maximum deviation from the neutral standing position occurred at 500ms, 1500ms, and 2500ms.

2.3.1.3 Procedure

The procedure for the study replicated Experiment 1a with the exception that each trial started with a 1000 ms black screen followed by the action-scene composite for 3000 ms where the action was performed three times and after the action-scene composite had been displayed a second 1000 ms black screen was displayed. In the 2AFC recognition task, where participants saw 40 test trials, each of which began with a 1000 ms black screen, a composite performed on the left half of the screen for 3000 ms, an interval of 1000 ms with a black screen followed by a second composite being performed on the right half of the screen for 3000 ms. All other elements of the study (foil composition and wording of questions) remained the same.

2.3.2 Results

A 3 (Foil Type) x 2 (Group) ANOVA was conducted. For group, there was no significant difference between sleep (M = 0.505, SE = 0.028) and wake (M = 0.540, SE = 0.026), F < 1, *p* = ns. There was also no significant difference based upon foil type, F < 1, *p* = ns, and no interaction between group and foil, F < 1, *p* = ns. Comparing overall proportion of items correctly recognised between Experiment 1a (1 action repetition) and Experiment 2 (3 action repetition; Figure 3.3) resulted in no significant difference, F < 1, *p* = ns. There was also no significant difference of experiment by group, experiment by foil type, or experiment by foil type by group interaction, all F < 1, *p* = ns.

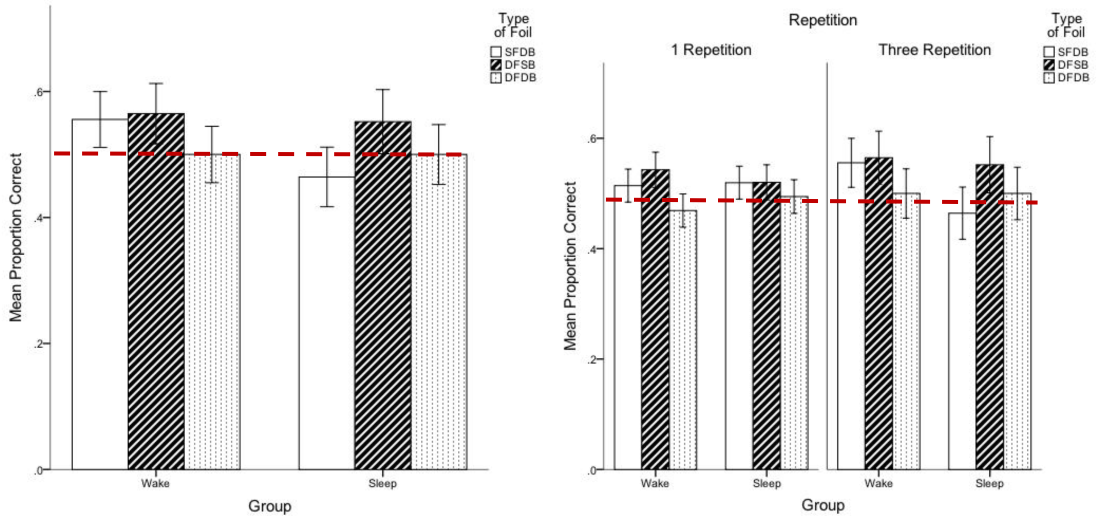


Figure. 3.3. Left panel shows a graph showing the average accuracy for each group. Bars indicate mean proportion correct by type of foil, SFDB- Same Foreground Different Background; DFSB- Different Foreground Same Background; DFDB- Different Foreground, Different Background. Errors Bars are ± 1SEM.

Right panel shows a graph showing the average accuracy for each experimental group compared across Experiment 1a and Experiment 2. Bars indicate mean proportion correct by type of foil, SFDB- Same Foreground Different Background; DFSB- Different Foreground Same Background; DFDB- Different Foreground, Different Background. Errors Bars are ± 1SEM.

Within the last two experiments we examined the role of sleep on action-scene composite recognition. Previous literature has demonstrated that action-scene recognition is prone to errors, with recognition of specific pairs at approximately chance level (Urgolites & Wood, 2013b). One of the suggestions for this difference is due to actions and scenes being processed in different cortical areas, with these disparate locations part of the reason for the difficulty in relational binding (Urgolites & Wood, 2013b). In order to test a cortical location hypothesis, we used object-scene composites as stimuli, which are also thought to be located in separate cortical locations. If the issue of relational binding is one of disparate storage sites, there should be a similar issue of binding between object-scene stimuli.

2.4. Experiment 3a Sleep’s role in object-scene Relational Binding: Sleep/Wake effect

2.4.1 Method

2.4.1.1 Participants

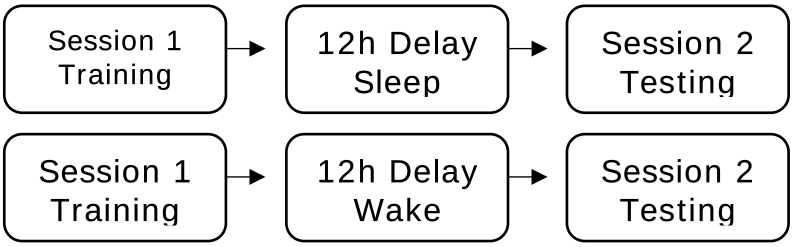
A total of 40 undergraduate participants (27 females, 13 males, mean age =19.25, SEM= 0.03) with normal or corrected to normal vision were assigned to groups in a similar way to Experiment 1a. Participants were asked to maintain a normal sleep schedule for the two days prior to testing, to sleep for at least 6h for the night preceding the study, and to refrain from drinking alcohol and caffeine for at least 12h prior to the start of the study. Participants reported mean bed times of 11.36pm, wake times of 8.14am, and average sleep times of 8h 38m. Participants were either given course credit or were paid £7 for participating upon completion of the study after the second session. Participants gave informed consent and were reminded they were free to withdraw from the study at any time without incurring penalty.

2.4.1.2 Stimuli

The stimuli consisted of 40 animated objects and 40 images of scenes that were combined to create 40 object/scene composites. The objects were taken from a previous paper that had examined fidelity of objects in VLTM by Brady et al. (2008) whilst the scenes were taken from a study examining the fidelity of scene representations in VLTM by Konkle et al. (2010). The combined composites were taken from a previous study by Urgolites and Wood (unpublished). Each composite consisted of an object rotating a full 360° for 1 second within one scene (see Figure 3.4.). The objects appeared in the centre of the scene. All of the objects had the same duration (1000ms) and frame rate (30 frames per second) with each object reaching its maximum deviation from the neutral, face-on position at the 15th frame rotating 180°. The object stimuli included household appliances, electronics, vehicles, and fruit or vegetables. The scene stimuli used in these composites was the same as experiment 1a. The study was programmed on Psychopy 1.83.05 (Peirce, 2009). Foils were created in the same ratio of 13/13/14 as in Experiments 1 and 2.

2.4.1.3 Procedure

The procedure was the same as Experiment 1a with the exception of object-scene composites appearing instead of action-scene composites and a delay of 12h between training and testing.



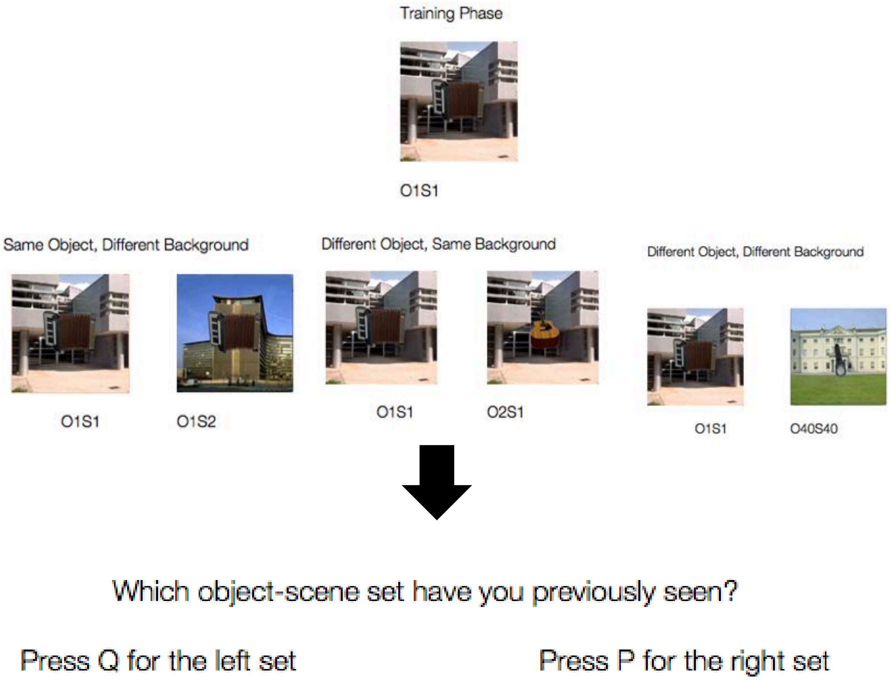


Figure 3.4 Image demonstrating the study and test phase of the object-scene composite recognition task.

2.4.2 Results

A 3 (Foil Type) x 2 (Group) ANOVA was conducted. There was a main effect of group, F(1, 39) = 9.527, p = 0.002. Sleep (M = 0.644, SE = 0.017) had a beneficial impact on object-scene recognition compared to wake (M = 0.570, SE = 0.017). The observed accuracy levels did significantly differ from chance performance, sleep group t(19) 8.405, $p < 0.001$, wake group t(19) 3.924, $p < 0.001$.There was also a main effect of Foil Type, F(2, 38) = 9,214. p < 0.001. Post-hoc analysis revealed that SFDB (M = 0.672, SE = 0.021) was significantly more accurate than DFDB (M = 0.546, SE = 0.021), p < 0.001. There was no significant difference between DFSB (M = 0.603, SE = 0.021) and SFDB, p = 0.065, or DFDB, p = 0.155. There was no significant interaction between group and foil type, F(2, 38)= 1.721, p = 0.179.

2.5. Experiment 3b Sleep’s role in object-scene Relational Binding: Control Groups

As we noted a sleep/wake effect within Experiment 3b in order to control for circadian effects a second object-scene study was conducted using an immediate recognition task. This also served as a comparison of immediate recognition to the action-scene task.

2.5.1 Method

2.5.1.1 Participants

40 undergraduate participants (27 females, 13 males, mean age =19.2, SEM= 0.03) with normal or corrected to normal vision were randomly assigned groups in the same manner as outlined in experiment 1a. Participants were asked to maintain a normal sleep schedule for the two days prior to testing, to sleep for at least 6h for the night preceding the study, and to refrain from drinking alcohol and caffeine for at least 12h prior to the start of the study.

Participants reported mean bed times of 11.51pm wake times of 8.43am and average sleep times of 8h 38m. Those in the control group were given course credit or £3.50 for completing they study. Participants gave informed consent and were reminded they were free to withdraw from the study at any time without incurring penalty.

2.5.1.2 Stimuli

Stimuli used for the study were the same as those in Experiment 3a.

2.5.3 Procedure

Participants were randomly assigned to either a morning (9am) or evening condition (9pm). Initially participants completed the Stanford Sleepiness scale and completed a questionnaire about their sleep habits and any caffeine/alcohol intake in the last 12h. Participants then completed the study phase as outlined in experiment 3a. After completing the study phase, 1 minute later participants completed the test phase whereby participants had to indicate which object-scene composite had been previously displayed.

2.5.2 Results

A 3 (Foil Type) x 2 (Group) ANOVA was conducted. For Group there was no significant difference between Morning (M = 0.728, SE = 0.052) and Evening (M = 0.692, SE = 0.055), F(1, 39) = 2.533, $p = 0.112$. The observed accuracy levels did significantly differ from chance performance, morning group t(19) 14.790, $p < 0.001$, evening group t(19) 11.373, $p < 0.001$. There was a significant effect of Foil Type, F(2, 38) = 9.826, $p < 0.001$, with SFDB (M = 0.773) being significantly more accurate than both DFSB (M = 0.704), $p = 0.043$, and DFDB (M = 0.652), $p < 0.001$, while DFSB and DFDB did not significantly differ, $p = 0.173$. There was no significant interaction between Group and Foil ty[e, F < 1, p = ns. As with Experiment 1, performance in the immediate recognition task (Exp. 3b) was compared against performance in the delayed recognition task (Exp. 3a, see Figure 3.5 for comparison across experiments). Analysis revealed that there was a significant difference based on recognition task delay, F(1, 79) = 38.820, *p* < 0.001, with the immediate recognition task (M = 0.710, SE = 0.012) significantly more accurate than the delayed recognition task (M = 0.607, SE = 0.012).

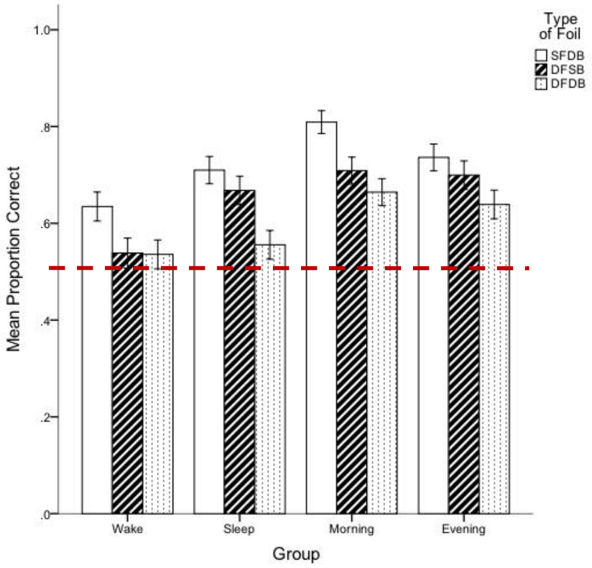


Figure 3.5. Graph showing the average accuracy for each experimental group. Errors Bars are ± 1SEM.

3. General discussion

To recap, previous literature suggests that the VLTM is capable of supporting a large amount of high-fidelity representations of actions (Urgolites & Wood, 2013a), objects (Brady et al., 2008), and scenes (Konkle et al., 2010a, 2010b), and that when presented in a composite image (e.g., object in a scene), object recognition is further enhanced by scene presentation (Davenport & Potter, 2004; Vogt & Magnussen, 2007), similar to the encoding-specificity principle (Tulving & Thomson, 1973). However, few studies have explored specific composite recognition in a 2AFC paradigm (that is to recognise a specific item-scene composite when presented with an alternative). One such study, Urgolites and Wood (2013b), observed that recognition for specific action-scene composites was difficult, with recognition accuracy at approximately 59% (with chance at 50%), despite recognition of specific actions or scenes at close to reported levels, suggesting an issue of relational binding between the two items. As sleep has been demonstrated to be beneficial for consolidation of learned associations (see Diekelmann & Born, 2010; Rasch & Born, 2013), the current examined if sleep could have any benefit on recognition of action-scene, and object-scene composites.

Focusing on action-scene binding first, the results appear consistent with the existing literature. In Experiment 1b, participants in the control groups who completed the recognition task immediately after learning had proportion of items correctly recognised at approximately 55%, significantly above chance but still lower than individual item recognition, in line with Urgolites and Wood (2013b). Furthermore, Experiment 1a demonstrated that sleep had no beneficial effect on consolidation, with proportion of items correctly recognised in both the sleep and wake groups not differing significantly from chance. When action-scene composites were presented with the action repeated three times and a delay between exposure and test (Experiment 2), proportion of items correctly recognised was again at chance levels and did not significantly differ from Experiment 1a. There was a significant difference in time of recognition task, with proportion of items correctly recognised in the immediate recognition task (Experiment 1b) significantly higher than in the delayed recognition task (Experiment 1a), suggesting that despite accuracy being close to chance, when tested immediately recognition of action-scene composites is possible, but is prone to decay.

In contrast to the action-scene tasks, for the object-scene task (Experiment 3a) there was a significant benefit of sleep with proportion of items correctly recognised in the sleep group (M = 0.644) significantly higher than the wake group (M = 0.570), although these were significantly lower than the immediate recognition groups (Experiment 3b), suggesting that although object-scene composite representations are prone to decay. Moreover, in the immediate recognition task experiments (Experiment 1b, 3b) the object-scene recognition was significantly higher than action-scene recognition, suggesting that there is a qualitative difference between the two, which to the authors' knowledge is the first study to demonstrate this.

There is a significant difference in consolidation of action-scene composites compared to object-scene composite; recognition for object-scene was significantly more accurate than action-scene composites in both experimental (12h delay between sessions) and control conditions (2 min delay between sessions), as such, the first question is does this difference occur? One suggestion we can dismiss is the limited amount of exposure time to stimuli affecting the actions and object separately. Within both Experiment 1 and 3 participants were only exposed to the target stimuli for 1000ms. While object recognition is fast, with brain responses associated with visual discrimination of objects occurring around 150ms (Allison et al., 1999; Thorpe et al., 1996), action recognition within the current study is not possible until 500ms (where the action reaches maximum deviation from the neutral standing position, making what action it is clearest) yet this did not appear to affect the results. Accuracy for the repeat detection task in the training phase was consistently high across all experiments regardless of stimuli type, averaging over 90% with no significant difference between exposure for 1000ms and exposure for 3000ms, suggesting that participants could accurately recognise the specific composite under certain conditions, consistent with the previous literature (Urgolites & Wood, 2013b) recognition of that specific item-scene composite; as the repeat detection task is presented as a Yes/No judgement task, familiarity based recognition of just one element would suffice in making a correct judgement.

Instead, the significant difference between action-scene and object-scene composites appears in the recognition task when the target composite is presented alongside a foil. Before discussing the details between the two it is worth noting that although actions and objects are often compared, both within the current study and the wider literature, particularly that of eyewitness testimony (Brown & Deffenbacher, 1978; Kersten & Earles, 2010), they are fundamentally different forms of stimuli, with differing levels of complexity, thus different forms of memory. Actions, by virtue of being a movement, occur in both a spatial and temporal form, whereas objects only occur in a spatial manner. As such caution should be taken in interpreting results when they are compared directly.

When participants engaged in the 2AFC task proportion of items correctly recognised declined to close to chance levels in the action-scene task, consistent with previous literature (Urgolites & Wood, 2013b) but recognition of specific composites was significantly higher in the object-scene task. In their paper Urgolites and Wood (2013b) suggest that the difficulty in action-scene binding was potentially due to the separate storage of actions and scenes within the VLTM, with the binding at retrieval problematic due to the requirement of having to draw representations from separate cortical locations. However, as both objects and scenes are also stored separately within the VLTM (see Kravitz et al., 2011), location of stored representations may not be an adequate explanation for the observed difference. Furthermore, as the same background-scene stimuli was used across all experiments, this suggests that any issue of binding is related to the foreground item - the action or the object.

One possible explanation for the difference may be related to the form of encoding and consolidation of items through perceptual and conceptual features. There is an extensive literature that suggests that conceptual knowledge can have a beneficial role in consolidation within the VLTM (Brady et al., 2011; Konkle et al., 2010b). Within the current study, by having a conceptual representation based upon past experience, this may reduce the cognitive load during initial encoding. Reducing the cognitive load would mean that participants can engage in directing their attention and encoding resources to the details that are most likely to distinguish between pairs (e.g., Eysenck, 1979; Nosofsky, 1986). The concept of using features to distinguish items (termed *Diagnostic Feature Support*) is well established in distinctiveness models of memory (Nairne, 2002; Hunt & Worthen, 2006; Schmidt, 1991), and models of categorisation (Nosofsky, 1984, 1986; Anderson, 1991).

In contrast, as actions are novel and thus don't have any pre-existing conceptual knowledge, encoding and consolidation of the representation is dependent on perceptual features (e.g., arm movement), allowing participants to create high-fidelity representations of the individual actions within the hippocampal store that can be recognised in subsequent recognition tasks but at the expense of creating a consolidated association with the scene. This process may be aided by the mirror neuron process, whereby viewing an action can trigger the same neuronal firing pattern in the parieto-frontal section of the brain than when performing the action (see Steinhorst & Funke, 2014) but this still requires attention to the action for its duration, thus it appears to not help relational binding in the same manner preexisting conceptual knowledge can help objects at encoding. This view would support the result observed by Urgolites & Wood (2013b) who observed that separate action and scene recognition was close to previously reported levels (~80%) while the composite recognition was only just significantly above chance.

This difference in encoding does appear consistent with recent literature on hippocampal role in episodic memory. In the past few fMRI studies into the hippocampus have identified numerous functions, including *pattern separation* within the Dentate Gyrus and *pattern completion* within the CA3 hippocampal region. Pattern separation refers to the hippocampus' ability to form distinct, non-overlapping representations of highly overlapping input. For example, Chadwick and colleagues presented participants with a series of videos containing overlapping foreground and background stimuli (e.g., taking the current study example, a1s1, a2s2, a1s2, a2s1) and pattern analyses of the fMRI data revealed that their representations in the hippocampus can be distinguished (Chadwick, Hassabis, & Maguire, 2011). In contrast, pattern completion refers the ability to retrieve a complete representation (pattern) based upon partial input. For example, you can recall all the information about a person just by hearing their name or seeing their picture. Horner and Burgess (2014) examined the role of pattern completion in bound representations through the use of location-object-person associations. They observed that cueing with location allowed the retrieval of both the associated person and object representations, with the cueing correlating with hippocampal activity in their respective cortical areas. However, the retrieval effect was specific to category and not the specific element (e.g., location may cue *person*, but not *Jose Mourinho*), thus it is unclear if cueing led to reinstatement of specific elements or just general concept. Recent literature on these hippocampal functions suggest they may work in tandem with CA3 through the feedforward mechanisms displaying output for both pattern separation and pattern completion.

When applying this form of pattern separation/completion to the current study, the distinction between action-scene/object-scene recognition appears to be explainable. Within the action-scene composite pattern separation allows retrieval and recognition of high-fidelity representations, accounting for the previously seen result of Urgolites and Wood (2013b). However, if pattern completion is in some part mediated by reinstatement of category and not specific element (Horner & Burgess, 2014), then actions, which are more generalised and don't have the semantic label for specific exemplar-level actions, would be more susceptible to interference from the foil composite that are from the same category. In contrast, the object-scene composites are able to engage in both pattern separation allowing individual item recognition but also pattern completion, with the effect of category level reinstatement mitigated by the presence of pre-existing exemplar-level object prototypes. As such, the pattern completion process is expedited as it requires level visual input than the action-scene composites.

Furthermore, when examining the difference between the action and object scene stimuli, this may also be linked to language. Previous literature has demonstrated that labelling visual items in a way that can relate to conceptual knowledge can aid consolidation and recognition of novel visual items (Wiseman & Neisser, 1974; Koutstaal et al., 2003). For example, Wiseman and Neisser (1974) presented participants with two-tone ambiguous faces and required participants to judge whether or not it was a face. In a subsequent recognition task memory for previously seen items was significantly higher among items judged to be faces than those that were not labelled. Similarly, in a series of experiments Koutstaal et al. (2003) recognition of ambiguous shapes increases when a disambiguating semantic label is provided during training, and memory for real-world objects is better than memory for highly-distinct but novel items. Within binding literature, Dessalegn and Landau (2008) observed that verbalisation of the bound items (e.g., *The red square is next to the green circle*) aided consolidation of the bound representation in a matching task for 4-year olds, with no such improvement observed with nonlinguistic cues.

As such, it may be that the exemplar-level semantic label for objects that exists as part of the pre-existing conceptual knowledge may lead to expedited encoding and consolidation of the individual item (see Brady et al., 2011), thus allowing associations to form not on a pure visual level, but on a visual-semantic level, with participants consolidating the association of two exemplar-level semantic labels (e.g., banana-beach) alongside the visual representations. In contrast, as the actions are novel, they have no clearly defined exemplar-level semantic labels to aid encoding or consolidation at an associative level. It may be that alongside a pure visual association, the visual semantic level is one of category-exemplar (e.g., a jump – beach), thus in the 2AFC task the foil stimuli that contains previously seen stimuli in novel pairings may act as interference to a greater level.

Beyond the difference between action-scene and object-scene composite recognition, the novel result of the paper was the observed result that sleep preferentially aided consolidation of specific object-scene composites compared to an equivalent period of wake. The result adds to a growing literature that has demonstrated that sleep can aid consolidation of associative memory (Chatburn et al., 2014), with previous literature demonstrating a sleep-based consolidation effect amongst related- and unrelated-word pairs (Gais & Born, 2004), item-context association (van der Helm et al., 2011), and face-location pairs (Ruch et al., 2012).

First, the general decrease in action-scene composite recognition may reflect a natural decay of the fidelity of the action representation. As the action is novel with no form of semantic label recognition is based primarily off of perceptual features, which can degrade in memory representation over time as it shifts to a more conceptualised representation. If we apply the categorical reinstatement effect at pattern completion as seen in Horner and Burgess (2014) this would further explain chance level performance, the participants no longer have a high-fidelity representation of the action available in episodic memory and categorical reinstatement may apply to both items in the 2AFC task.

For the object-scene composite task, although the target item representation may decay over the same time frame, because there are already prototype item representations available (Konkle et al., 2010b) then retrieval of the exact item is not as important as pattern completion can occur through the use of the item prototype as it retains enough unique features to still appear as the target item. The difference between sleep and wake groups for the object-scene composite may reflect consolidation of that particular learned association. Although previous literature suggests that in part sleep can aid gist extraction/abstraction of memory, this is not as essential to object-scene composites that again can utilise the item prototype representation as a gist form of the item in the associative task.

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Chapter 4. The impact of sleep on the recall of different item modalities in a free recall task

Within the previous chapter it was demonstrated that object-scene composite recognition was significantly more accurate than action-scene composite recognition, in both immediate recognition tasks and after a delay containing sleep or wake. While this is a novel result, the stimuli used may not truly be applicable to real world scenarios. Items (actions/objects) were presented in front of a scene but this contained no form of contextualisation, something that has been suggested to aid encoding, consolidation, and retrieval of actions (e.g., Kersten, 1998). As such, the following chapter seeks to implement this contextualisation of the item modalities and examine the effect of sleep on consolidation. To apply this to real-life scenarios this was implemented as recall tasks of CCTV footage of crimes in order to mimic eyewitness testimony. The study focuses on four key item modalities, Actions, Objects, People, and Locations.

Article prepared to standard of submission to journal.

The impact of sleep on the recall of different item modalities in a free recall task

Abstract

In eyewitness testimony the details matter. The distinction between a man with blonde hair and blue eyes attacking a man rather than a man with blonde hair and brown eyes may be the deciding factor in convicting an innocent man who just happened to also witness the incident. These 'action-agent' binding errors are commonplace, but can sleep help? The current study seeks to see if sleep can aid in consolidation of multi-item complex events in the form of CCTV crime recall. Participants viewed 6 CCTV videos and completed a free recall task for each video in two sessions, with the second session 12h after the first and containing a period of sleep or wake. Details regarding actions, objects, people, and locations were recorded. There was a significant difference between item modalities, with actions recalled more frequently than other item modalities. However, there was no sleep/wake effect, suggesting that a 12h delay is still sufficient time to recall accurate details of witnessed events. These results suggest that sleep had no significant effect on consolidation of different item modalities. The results are discussed in relation to the existing literature of sleep and eyewitness testimony.

Keywords: Sleep, Eyewitness Testimony, Item Modality

Highlights

- Actions were recalled to a higher frequency
- No effect of sleep on recall of information

1. Introduction

Despite literature demonstrating that humans have a large and detailed memory (Brady et al., 2008; Standing, 1973; Konkle et al., 2010), it is often prone to distortions (Schacter, 1996). Evidence from eyewitness testimony reveals that people are susceptible to errors of agent-action binding; mistakenly recalling actions and agents from two different events as being from the same event (Earles, Kersten, Curtayne, & Perle, 2008; Kersten & Earles, 2010; Kersten, Earles, Curtayne, & Layne, 2008; Loftus, 1976; Perfect & Harris, 2003; Ross, Ceci, Dunning, & Toglia, 1994). A similar issue is that of unconscious transference errors; whereby a witness to a crime can be mistakenly be identified as a perpetrator in later police line ups due to occurring in the same situation (Brown, Deffenbacher, & Sturgill, 1977; Buckhout, 1974; Loftus, 1976), suggesting an issue at retrieval.

These issues of omission/commission are often linked to false memories; commonly defined as the memory for an event that did not exist or existed in a different way as to how it occurred. Within the laboratory setting these are often created through the Deese-Roediger-McDermott (DRM) paradigm (Roediger & McDermott, 1995); participants are presented with a list of thematically related words (e.g., bed, dream, dark, night, snooze, pillow) then in subsequent recall or recognition tasks often report an unseen critical lure which is thematically related to the list of words (for the above example- *sleep*). A similar effect can be generated in autobiographical memory, for decades research using the “lost in the mall” paradigm has demonstrated that adults can falsely recall autobiographical memories ranging from non-existent hospital stays, animal attacks, and even hot-air balloon rides (for a summary, see Newman & Garry, 2013). Applied to eyewitness testimony, these false memories are often generated through the misinformation effect. Within this paradigm participants experience an event, receive post-event misinformation, and in a subsequent memory task often reported events altered by the misinformation (Loftus, 2005; Loftus & Hoffman, 1989). Theories for this range from the post-event misinformation reflects retroactive interference, it impairs access to the original memory trace (Loftus, Miller, & Burns, 1978), or the misinformation causes issues around source monitoring with participants unable to accurately recollect which source is the correct one (Lindsay & Johnson, 1989), with this theory supported by recent brain imaging studies (Okado & Stark, 2005; Stark, Okado, & Loftus, 2010). A recent comparison between DRM based false memories and the misinformation effect by Zhu, Chen, Loftus, Lin, and Dong (2013) demonstrated a small but significant positive correlation between the two, although Zhu et al. suggest it is only their global discrimination ability (those susceptible to misinformation are also likely to be susceptible to DRM task) that is linked between the DRM paradigm and misinformation susceptibility.

Issues of memory errors therefore present an important practical issue; accurate recall of key information such as actions performed, objects used, people involved, and location of the incident are crucial in criminal investigations and witness statements (Woolnough & MacLeod, 2001), yet they are susceptible to manipulation relatively easily (Frenda, Nichols, & Loftus, 2011; Nash & Wade, 2009). For example, Shaw and Porter (2015) interviewed undergraduate students about a true event from their past and a non-descript false event involving the police. After three interviews 70% of participants reported false memories of committing a crime that led to police interaction, although the methodology of the study has been questioned for failing to distinguish between false memories (genuinely remember the event) and false belief (accept it may have happened), an important distinction in the literature and when applied to the Shaw and Porter experiment, false memory generation is approximately 22%, suggesting that it wasn’t false memories driving the effect observed by Shaw and Porter, but a belief it *may* have happened. (Wade, Garry, & Pezdek, 2017).

One area that is underreported in the literature is consolidation of these different modalities of information in a combined presentation. As previously stated in the first paragraph, the existing literature demonstrates that we have a remarkably large and detailed capacity for objects (Brady et al., 2008; Standing, 1973), scenes (Konkle et al., 2010), and actions (Urgolites & Wood, 2013a), yet few have directly compared across the different item modalities within the same study. Within one study, Urgolites and Wood (2013b) presented participants with combined action and scene composites and in a subsequent recognition task 1 minute after exposure participants were presented the original set and a foil set with participants required to identify the specific composite. They observed that for individual action or scene recognition, accuracy was at previously reported levels (averaging 80%) but when required to identify the specific composite, accuracy was close to chance (59%), suggesting that while humans are capable of binding actions and scenes together, it is prone to error, with Urgolites and Wood theorising that actions and scenes may be stored in separate locations and require “rebinding” at retrieval. In a similar experiment Old and Naveh-Benjamin (2008) examined participants’ ability to recognise people, actions, and specific people-action composites. After a short delay participants were most accurate for actions (70%), then person-action association (47%), then person (39%), with a retest the following day replicating the difference, a result confirmed by Kersten et al. (2008). One key study by Deffenbacher, Carr and Leu (1981) examined the effects of retroactive interference after two minutes and two weeks on different item modalities, faces, objects, landscapes (scenes), and words. Within the study Deffenbacher et al. sought to understand the role of new information on inhibiting retrieval previously learned material (*retroactive interference*), an important issue in eyewitness scenarios where interviews may occur some time after the event. They observed that after two minutes, recognition was above chance for all item modalities and retroactive interference only significantly affected faces and landscapes. When retested after 2 weeks, retroactive interference had no significant interaction with item modality but interestingly memory for faces was the highest accuracy out of the four tested, a result which highlights that in eyewitness testimony memory for people at the event can persist, but associated information such as the actions the people performed decays, possibly giving rise to the previously mentioned action-agent binding errors (Earles et al., 2008; Kerstern & Earles, 2010; Kerstern et al., 2008; Loftus, 1976; Perfect & Harris, 2003; Ross et al., 1994).

While these studies provide important evidence for different encoding and retrieval mechanisms for the different item modalities, memory was often measured by recognition tasks, a qualitatively different process than free recall that is primarily used in eyewitness testimony (Migueles & Garcia-Bajos, 1999). In studies utilising free recall tasks, accuracy for seen actions is high (Clifford & Scott, 1978) but not people (Tollestrup, Turtle, & Yuille, 1994). In a seminal paper, Yuille & Cutshall (1986) observed that free recall of an event typically consisted of actions (56%), people (26%) and objects (17%). Within the same task accuracy was highest for objects (87%) compared to actions (82%) and people (74%), again, suggesting differences in encoding and retrieval for each item modality, a result replicated by Migueles and Garcia-Bajos (2007) who observed that after viewing a crime participants accurately recalled 57% of action details and 38% of people details observed, suggesting that actions are among the most salient items at encoding.

Yet one aspect of research that has not been explicitly examined is the role of sleep in consolidation of these different item modalities. Extensive literature from neuroscience and behavioural psychology demonstrates that sleep aids memory consolidation (for a summary, see Diekelmann & Born, 2010; Rasch & Born, 2013), and has a beneficial impact on associative memory (for a summary, see. Chatburn et al., 2014). Models of sleep’s role in consolidation suggest that sleep aids consolidation in two ways- by passively reducing interference with existing memory traces, and by actively repeating activation of the encoded memory representation in the hippocampal network and subsequently integrating the representation into prior knowledge located within the long-term neocortical store. Yet these encoded representations undergo a qualitative change; alongside veridical memory consolidation, sleep has been demonstrated to promote consolidation of “gist” based memory, promoting shared categorical elements and themes of newly encoded memories for easier integration with pre-existing information (Durrant & Lewis, 2009; Gomez et al., 2006; Lewis & Durrant, 2011; Sio, Monaghan, & Ormerod, 2013; Wagner et al., 2004). While beneficial for integration, promotion of gist-based memory can lead to false memories within the DRM paradigm (Diekelmann, Born, & Wagner, 2010; Monaghan, Shaw, Ashworth-Lord, & Newbury, 2016; Pardilla-Delgado & Payne, 2017; Payne et al., 2009; Shaw & Monaghan, 2017).

These effects are not limited to DRM-generated false memories, literature has demonstrated that participants often have prior knowledge of what is characteristic for each crime (Smith, 1991; 1993) and often have event-schemas (Greenberg, Westcott, & Bailey, 1998; Holst & Pezek, 1992; List, 1986) that can affect encoding and retrieval of witnessed events. In a series of studies, Garcia-Bajos and Migueles demonstrated this effect whereby participants were susceptible to false memories of witness events based upon typicality of the content within its event-schema; high-typicality content (e.g., perpetrator had a gun) was reported more often than low-typicality (e.g., perpetrator had a dog with them) and in subsequent recognition tasks high-typicality was falsely recognised more frequently than low-typicality. When participants were tested one week later, false alarms for low typicality reduced significantly (0.18 v .04) while high-typicality remained constant (0.44 v .45), suggesting that over time we are more susceptible to information that is more consistent (high typicality) with pre-existing schematic knowledge (Garcia-Bajos & Migueles, 2003, 2005). One study that has addressed the relationship between sleep and eyewitness testimony (Thorley, 2013) observed that decreased sleep quality and related increases in sleepiness reduced accuracy in recollecting peripheral details of a previously seen crime while central details remained unaffected, emphasising that sleepiness and sleep deprivation can impair peripheral recollection, although as this study only focused sleep related details on immediate recall, it is unclear what effect intervening sleep will have.

To the author’s knowledge few, if any, studies have addressed the role of sleep on these different item modalities when presented in a naturalistic free recall task. As of yet only one study has attempted something similar; the binding memory study in chapter 3 replicated the methodology of Urgolites & Wood (2013b) but modified it to include sleep and wake conditions as a factor, alongside a second study using a set of object-scene composite stimuli. Participants were assigned to a sleep or wake group and in the first session viewed 40 novel action-scene composite sets and after a delay completed a two-alternative forced choice recognition task to measure specific bound memory representations (i.e., recognition of a specific action/specific background pairing). Within the action-scene experiment sleep had no beneficial effect on recognition, decreasing proportion of items correctly recognised to chance levels, similar to the wake group, suggesting that any form of delay was a detriment to action-scene recognition. In contrast, within the object-scene experiment sleep preferentially preserved object-scene bound representations (64.4%) compared to the wake group (57%). However, as this was a recognition task it is unclear if this difference will be replicated in a free recall task. Moreover, the task was focused on actions, objects, and scenes; it is unknown what the effect of sleep may be on other modalities such as people when presented in combination. Within the current study participants were assigned to a sleep or wake group and in the first session viewed six CCTV videos of various crimes, completing a free recall question on each video after three videos. In the second session participants completed a free recall question for each video without viewing the videos again. We hypothesise that across both sessions actions should be recalled to a higher level than people, objects, and locations, in line with the previous literature (Old & Naveh-Benjamin, 2008; Kersten et al., 2008). We also hypothesise that sleep should have a beneficial impact upon consolidation across all item modalities compared to an equivalent period of wake, either due to lack of interference from encoding of new memories, or through actively consolidating the representation.

2. Methodology

2.1 Participants

41 participants (24 females, mean age = 19.84, SEM = 0.04) with normal or corrected to normal vision were randomly assigned to each of the 2 conditions (wake or sleep). Participants initially signed up to the study agreeing to be tested on two sessions twelve hours apart, then the experimenter assigned them their specific timeslot in order to avoid any potential time preferences in the participants. Participants were asked to maintain a normal sleep schedule for the two days prior to testing and were asked to sleep for at least 6h for the night preceding the study and refrain from drinking alcohol and caffeine for at least 12h prior to the start of the study. Participants reported mean bed times of 11:04pm, wake times of 7:53am, and average sleep times of 8h 49m.

Participants were either given course credits towards a first year module or paid £7 for participating upon completion of the study after the second session. Participants gave informed consent and were reminded they were free to withdraw from the study at any time without incurring any penalty. The research was approved by the University Research Ethics Committee.

2.2 Stimuli

2.2.1 Videos

6 videos, ranging from 30s to 2 minutes were used in the study. The videos involved criminal activity captured on CCTV posted on Youtube.com. All the videos included were not flagged as containing inappropriate content and none were age restricted. The first video was footage of a woman having her purse stolen in a car park by two males. The second video was of two males

robbing a small convenience store where a third male and a female are witnesses to the crime. The third video was of a female being attacked on public transport. The fourth video was of 2 males attempting to rob a post office. The fifth video was footage of 5 males breaking into a storage depot. The sixth video was of a female shoplifting from a phone store (See figure 4.1)

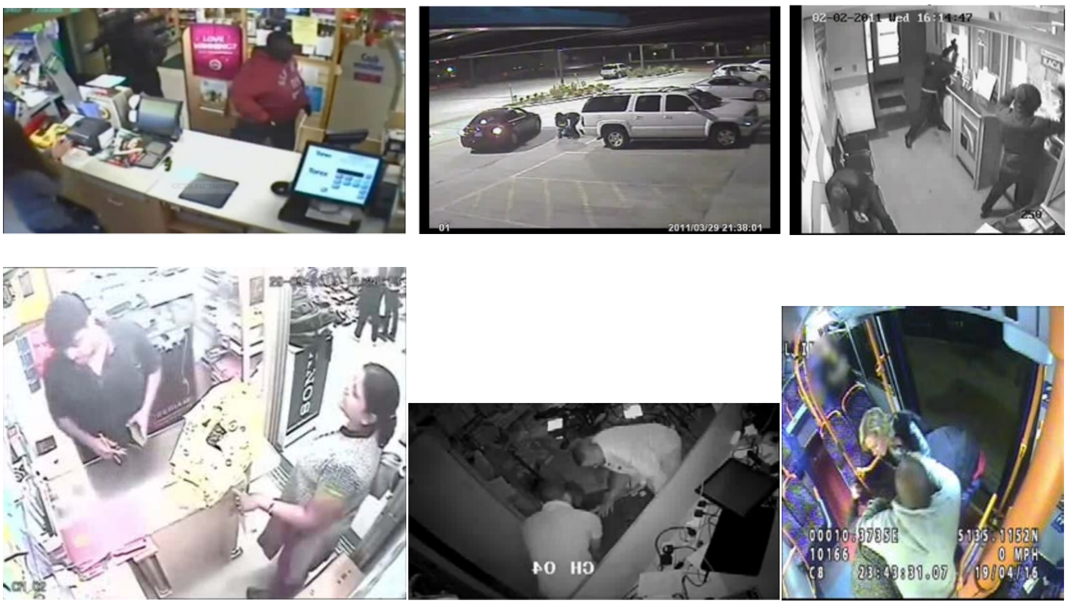

Figure 4.1 Video stills taken from 6 stimuli videos. Video length ranged from 30s to 2 minutes

2.2.2 Questionnaires

The questionnaire used in the study comprised a single, free recall question asking them to recall everything they could about the video including a prompt saying ‘Including the perpetrators, victims, the crime, the location, and any actions performed’, similar to other studies utilising a free recall paradigm (Gabbert, Hope, & Fisher, 2009). Participants were also given a questionnaire regarding sleep habits.

2.3 Procedure

Before attending the first session, participants were randomly assigned to one of two groups, a sleep group viewing the videos at 9pm then tested at 9am or a wake group viewing the videos at 9am then tested at 9pm.

For the first session participants first completed consent forms and after completing a questionnaire on sleep habits viewed the first three CCTV videos. After watching three videos participants were then prompted with the free recall questionnaire for each of the three videos. This procedure was then repeated for the next three videos. 12 hours later participants returned for the second session and were instructed to complete a free recall questionnaire for each video. In the second session participants were given a total of 30 minutes to complete the same questionnaire for each of the six videos. Participants did not view the videos again and no cues were given to participants about the content of the videos.

2.4 Scoring

Answers produced by free recall in the questionnaires were coded for information type in accordance within pre-existing coding guidelines based on the work of Memon et al. (1996, Memon et al., 1997; Wright & Holliday, 2007). Information was coded into four key categories: people (P), actions (A), objects (O), and locations (L). For example, a participant recalling “The man attacked the victim with a knife” would be coded as two person details (Man, Victim), one object (knife) and one action (attacked). For the purpose of this study only correct information (statements that contained information that was present in the video) was included in subsequent analysis. Information was recorded for each individual video split by modality as well as each modality totalled across all videos.

3. Results

3 participants were excluded from the analysis due to not returning for the second session or failing to answer anything of content in response to at least 3 of the videos in the second session. To account for variance across the different

modalities of information and differences in potential detail available in each video, a 2 (Group) by 4 (Item modality) by 6 (Video) MANOVA was conducted with number of information recalled the dependent variable.

First a MANOVA was conducted across both session 1 and session 2 in order to determine any overall effect of item modality. Overall there was a significant effect of item modality, F(3, 34) = 149.345, *p* < 0.001, eta = 0.929. Post-hoc analysis revealed that actions (M = 8.52, SE = 0.44), people (M = 5.42, SE = 0.32), objects (M = 4.27, SE = 0.24), and location (M = 0.299, SE = 0.16), were all significantly different from each other, all *p* < 0.001, with this pattern replicated in both session 1 and session 2.

In order to account for differences between sessions, a 2 (Group) x 4 (Modality) x 6 (Video) MANOVA reported the ratio of information recalled in session 2 compared to session 1 (value over 1 indicate more information in session 1 than session 2, values under 1 indicate less information recalled in session 2 than session 1). Overall there was a significant effect of item modality, F(3, 34) = 5.570, *p* = 0.003, eta = 0.330. Post-hoc analysis revealed that the only significant pairwise comparison was between object details (M = 0.910, SE = 0.031) and action details (M = 1.022, SE = 0.033) *p* < 0.001, with all other pairwise comparisons between people (M = 1.051, SE = 0.042), and location (M = 1.046, SE = 0.064) non-significant, all *p* > 0.2. There was also a significant effect of video, F(5, 32) = 6.813, *p* < 0.001, eta = 0.516 but no significant effect of group, F < 1, with both sleep (M = 1.125, SE = 0.058) and wake (1.075) similar (See table 4.1 for full summary of detail recall). In order to examine the difference between session 1 and session 2 post-hoc analysis was also conducted on the change in number of accurate details recalled. Paired sample T-test revealed that total object details significantly differed from session one (M = 26.132, SE = 1.664) to session two (M = 23.763, SE = 1.572), t(37) = 3.414, *p* = 0.002; and a significant difference between total people details from session one (M = 38.605, SE = 2.008) to session two (M = 36.710, SE = 2.227), t(37) =

2.079, *p* = 0.045. There was no significant difference between session one and two for action details or location details, both *p* > .5.

Analysing two-way interactions, there was no significant interaction of item modality by group, F < 1, suggesting that sleep did not significantly affect item modalities in different ways way. There was also no interaction of video by Group, F(5, 32) = 1.325, *p* = 0.279, eta = 0.172. Analysing the three-way interactions, there was no significant item modality * video * group, F(15, 22) = 1.097, *p* = 0.412, eta = 0.428.

Table 4.1. Table displaying the average recall for each item modality by session and ratio of information recalled from session 1 in session 2 (value over 1 indicate more information in session 1 than session 2, values under 1 indicate less information recalled in session 1 than session 2).

	Group					
	Wake			Sleep		
	Session 1	Session 2	Proportion	Session 1	Session 2	Proportion
Action Details	7.235 (0.543)	7.523 (0.641)	1.033 (0.042)	9.625 (0.637)	9.688 (0.752)	1.011 (0.049)
Location Details	2.758 (0.218)	2.727 (0.227)	1.019 (0.050)	3.302 (0.255)	3.177 (0.266)	.975 (0.058)
Object Details	3.720 (0.331)	3.394 (0.317)	.913 (0.041)	5.229 (0.389)	4.740 (0.372)	.907 (0.048)
People Details	5.750 (0.410)	5.242 (0.440)	.926 (0.032)	7.375 (0.481)	7.323 (0.516)	.981 (0.038)

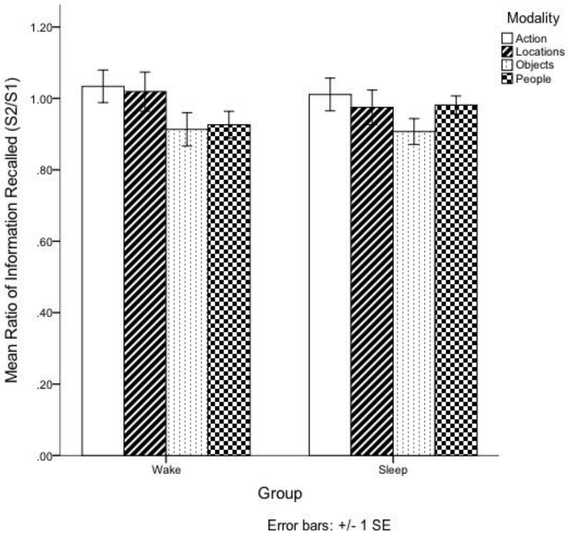

Figure. 4.2. Graph depicting mean number of details recalled for each Item modality split by group. Errors Bars are ± 1SEM.

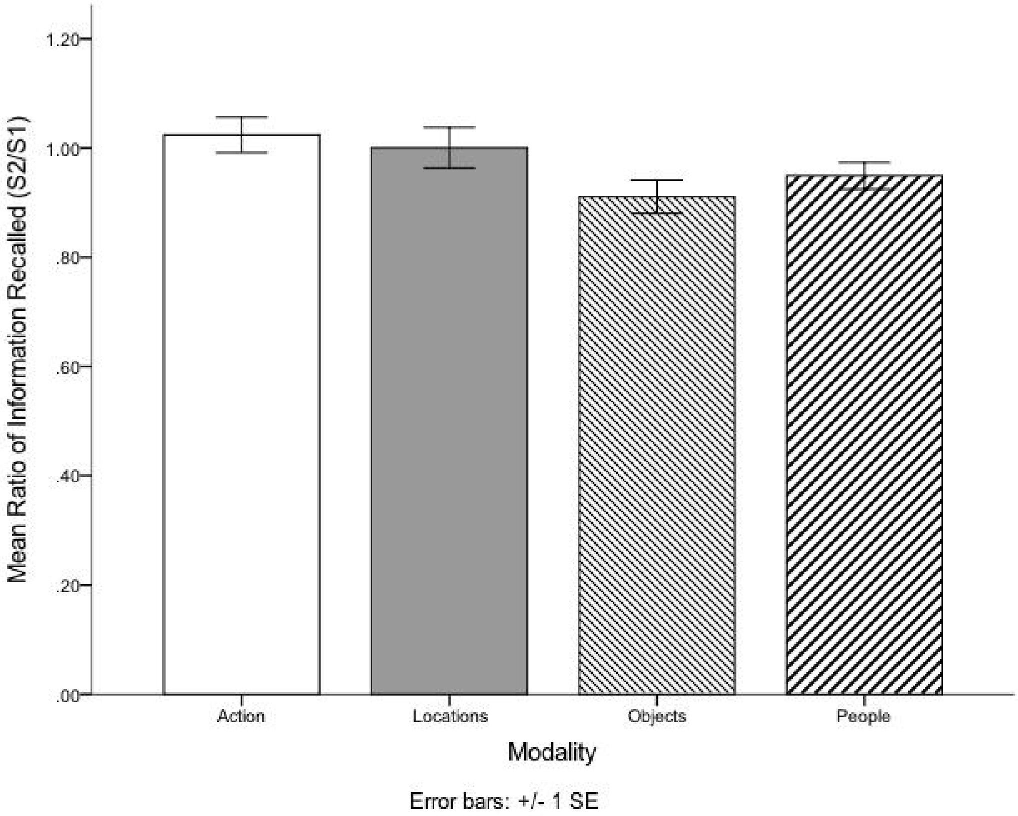

Figure. 4.3. Graph depicting mean number of details recalled for each Item modality across sleep and wake groups. Errors Bars are ± 1SEM.

4. Discussion

Previous literature suggests that autobiographical memory and eyewitness accounts of events are often prone to errors, either through post-event misinformation (Lindsay & Johnson, 1989; Loftus, Miller, & Burns, 1978) or due to schema based biases (Garcia-Bajos & Migueles, 2003, 2005), raising questions of the validity of any given account. While steps have been taken to ensure accurate recall, such as the Self-Administered Questionnaire (Gabbert et al., 2009), cuts to funding and increased time pressure often means witnesses are not always interviewed immediately after an event, with delays common (Kebbel et al., 1999; Kebbel & Wagstaff, 1999). As such, it is important to understand the impact of the beneficial role of sleep on consolidation of memory on such testimony. Within the current study we sought to examine the role of sleep in consolidation of different item modalities within eyewitness testimony of various crimes by measuring the number of action, objects, people, and location details. There was a difference based upon item modality, with action details recalled the most, then people, objects, and locations, but there was no significant Group difference; sleep had no beneficial effect on recall.

The results are an interesting extension of the current literature. First, participants were most accurate for actions, followed by people, then objects, and locations, with this pattern repeated across both sessions. The result adds to a growing literature on item modalities in recall. Previously, Old and Naveh-Benjamin (2008) observed that in a recognition task actions were significantly more likely to be recognised than person details, a result replicated by Kersten et al. (2008). Within recall tasks, the literature is more varied. While some studies have observed people and actions are recalled to a greater degree (Milne, Bull, Köhnen, & Memon, 1995), others have observed free recall elicits more object and action details (Memon et al., 1997; Granhag & Spjut, 2001). Although it seems conflicted, it can be explained; although efforts have been made to standardise stimuli, the types and amount of details remembered is also dependent on the stimuli used. For example, a video involving a single mugger and victim will naturally result in fewer person details compared to a multi-person fight. Similarly, the salience and meaningfulness of different detail types depends on the nature of the event (Akehurst et al., 2003). In the above example of a mugging, an event involving a large weapon will report more object details than a small weapon.

Our main hypothesis of the study was that sleep would aid consolidation of the memory for events compared to a similar period of wake. Recent studies examining sleep’s role in memory has found it is beneficial for consolidation of associations (Lewis & Durrant, 2011; Nadel et al., 2012, Walker & Stickgold, 2010; for a summary, see. Chatburn et al., 2014), both at a basic level such as associative pairs (Staresina & Davachi, 2008), and more complex associations, such as prediction of future outcomes (Djonlagic et al., 2009) and aiding complex problem solving (Sio et al., 2013). Recent models of sleep suggest that during sleep repeated activation of hippocampal networks repeatedly consolidate the representation (for a summary, see. Diekelmann & Born, 2010; Rasch & Born, 2013). Such models emphasise the role of spreading activation in memory consolidation; Lewis and Durrant's (2011) Information Overlap to Abstract (iOtA) Model suggests that as representations are repeatedly activated, shared categorical elements are preferentially strengthened through spreading activation, promoting schema-level memory formation. As several studies have highlighted the role of spreading activation in eyewitness testimony (Collins & Loftus, 1975; Paulo et al., 2016), we hypothesised that sleep may preferentially aid consolidation compared to an equivalent period of wake. Yet this was not the case, compared to an equivalent period of wake sleep had no significant benefit on proportion of information recalled from the first session, with no interaction with the item modality types either, going against our hypothesis. In the introduction we discussed the study reported in Chapter 3 as evidence that sleep does preferentially consolidate certain item modalities and based on that we thought we may be able to replicate the difference in the current study. Within their study it was observed that sleep had a beneficial effect on consolidation of object-scene composite recognition but not action-scene recognition, with Shaw and Monaghan theorising that prior knowledge and conceptual level "item prototypes" aided recognition of objects and scenes compared to actions. As such, why does this effect not appear here?

One explanation may be the level of detail that was required in the current study compared to the study in Chapter 3. In their study participants were required to identify specific composites in a 2AFC task, relying upon high-fidelity representations from long-term memory. In the current study by using a free recall task participants could retrieve information to a lower detail level than required in the binding task but in terms of accuracy, remain similar. For example, while participants in the action binding task of Chapter 3 may have been required to identify a jump with a twist to the left, in the current study participants could have said for the equivalent item the man jumped, meaning that a gist-based representation of the information would have sufficed as an accurate answer. Further studies would need to verify this, potentially though a similar methodology to that of Chapter 3 whereby participants are presented with a 2AFC containing a screenshot from the video and a foil screenshot containing some elements that have been changed. One study that has utilised a similar paradigm, albeit focused on false memory generation, is that of Lew and Howe (2016). In their study, participants were presented with visual scenes that contained schema-inconsistent information (e.g., a kitchen with a pan on a stool) and observed that at retrieval participants were more likely to falsely remember the schema consistent location (e.g., pan on the kitchen worktop), than the schema inconsistent. Although Lew and Howe's study is focused on item-location binding within a spatial context, it could be adapted for an expansion on the current study when designed in conjunction with the iOtA model (Lewis & Durrant, 2011) to examine the role of sleep in consolidation of schema-related information. One future adaptation could be to present modality-varied schema consistent/related/inconsistent videos of crimes (e.g., for *object,* a man being mugged with a knife/crowbar/crutch), and see if there are any differences based upon modality.

A second explanation for the lack of a sleep effect may be the result of methodological issues with the study. Within the current study participants were tested on recall on two occasions, immediately after viewing the videos and then after a 12h delay in order to compare the decrease in retrieval between groups. Yet, it may be that by implementing an immediate free recall task, this would mitigate any group difference. There is an extensive literature that has demonstrated that immediate retrieval of information can benefit subsequent recall (Bjork, 1988; Brock, Fisher, & Cutler, 1999; McCauley & Fisher, 1995; Shaw, Bjork, & Handal, 1995) in both learning information (Butler & Roediger, 2007; McDaniel & Masson, 1985; Wheeler & Roediger, 1992), and in eyewitness recall (Ebbesen & Rienick, 1998), similar to the widely known testing effect whereby being tested on information immediately after learning can benefit subsequent retrieval (Roediger & Karpicke, 2006a, 2006b). Ebbesen and Rienick (1998) observed that witnesses who had made an immediate recall attempt were less likely to suffer subsequent memory loss and recall performance was preferentially preserved over a retention interval of 4 weeks. This beneficial effect of recall may be explained through associative activation network models of memory; in actively retrieving the memory through a recall task the episodic memory representation is further strengthened (Anderson, 1983, Damasio, 1989). It is also theorised that through active retrieval participants are able to create different retrieval routes to information, offering more memory traces in order to access the episodic memory (Bjork, 1988; Schacter, Norman, & Koustaal, 1998). As such it may be that if participants didn't have the initial retrieval practice through the session 1 free recall task, we may have seen an effect of sleep compared to wake due to its promotion of associative memory, but this is a direction for future studies. The introduction of an initial recall task may also explain the increase in action details in the second session. When measured by proportion of information recalled from session one in session two, this pattern was replicated, actions were recalled significantly more often that people, objects, but not locations. In fact, the number of actions recalled in session two was often higher than in session one, something which did not occur for any other item modality. Again, this appears consistent within the eyewitness literature with Turtle and Yuille (1994) demonstrating that repeated eyewitness recall can lead to an increase in recall in subsequent recall attempts, similar to the benefits of retrieval practice. As actions were the most salient item modality across all videos, retrieval practice may have consolidated these further.

In summary, within the current study we sought to examine the role of sleep in consolidation of different item modalities. While we were able to replicate the existing literature that actions, objects, people, and locations can be recalled to differing levels (e.g., Old & Naveh Benjamin, 2008; Wright & Holiday, 2007), we were unable to observe any significant effect of sleep on consolidation, an effect the previous literature alludes to (for a summary, see. Diekelmann & Born, 2010; Rasch & Born, 2013), but part of the lack of an effect may be due to methodological issues, introducing an immediate free recall task enhancing subsequent recall through retrieval practice, reducing any effect of sleep v wake.

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Chapter 5. Lateralised sleep spindles relate to false memory generation

In the previous papers the primary focus has been on the role of sleep in associative memory in the consolidation of novel associations, best represented in the decontextualised object-scene/action-scene composite tasks. The results of the studies suggest that sleep is beneficial to consolidating these links, but they are somewhat dependent on prior knowledge. There is already an extensive literature on the link between associative memory and sleep architecture (e.g., hippocampal ripples, slow wave ripples, sleep spindles), the final study sought to expand upon this further, expanding the results of a pre-thesis study on the lateralisation of DRM-based false memories after sleep.

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Lateralised sleep spindles relate to false memory generation

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.

Key-words

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

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.

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 (for a summary, see 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 (for a summary, see. 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., Tamminen 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 (Tamminen 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

A total of 32 healthy, medication free university students (26 females; mean age = 19.72, SE = 0.30) 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 Stimuli

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 (Lavidor & Whitney, 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 5.1 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 in order to make our results comparable to previous literature.

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: $A' = 0.5 + ((H - FAF)(1 + H - FAF)) / (4H(1 - FAF))$ assuming $H \geq FAF$, 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 $H \geq FAF$, and $(FAF(1 - FAF) - H(1 - H))/(FAF(1 - FAF) + H(1 - H))$ when $FAF > H$.

False recognition: $A' = 0.5 + ((FAC - FAF)(1 + FAC - FAF)) / (4FAC(1 - FAF))$ assuming $FAC \geq FAF$, 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 $FAC \geq FAF$, 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, $F(1, 30) = 1.296$, $p = 0.264$, $\eta_p^2 = 0.041$, or hemisphere, $F < 1$, p = ns, but there was a main effect of word type, $F(2, 60) = 59.674$, $p < 0.001$, $\eta_p^2 = 0.665$, demonstrating the standard false memory effect, with unseen-new words (M = 0.224, SE = 0.025) resulting in significantly fewer false recognitions than unseen-lure words (M = 0.680, SE = 0.025, $p < 0.001$) which were recognised as old words not significantly different than seen-old words (M = 0.609, SE = 0.025, $p = 0.100$).

Table 5.1. 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	0.621 (0.045)	0.678 (0.034)	0.559 (0.045)	0.577 (0.034)
Unseen-New	0.229 (0.057)	0.125 (0.059)	0.282 (0.057)	0.261 (0.059)
Unseen-Lure	0.802 (0.057)	0.677 (0.049)	0.572 (0.057)	0.667 (0.049)

Also as predicted, there was a significant word type by group interaction, $F(2, 60) = 3.229$, $p = 0.047$, $\eta_p^2 = 0.097$. Simple main effects analyses revealed this was due to the wake group (M = 0.619, SE = 0.046) identifying fewer lure words as previously appearing than the sleep group (M = 0.759, SE = 0.037), $F(1, 30) = 5.438$, $p = 0.025$ $\eta_p^2 = 0.156$, again replicating previous observations of sleep increasing false memories. There were no significant differences in unseen-new, $F(1, 30) = 1.544$, $p = 0.224$ $\eta_p^2 = 0.049$, or seen-old, $F(1, 30) = 3.433$, $p = 0.074$ $\eta_p^2 = 0.103$, word recognition rates between the wake and sleep groups (see Figure 5.1). There was no significant hemisphere by group interaction, *F*(1, 30) = 3.497, *p* = 0.071, η_p^2 = 0.104, or hemisphere by word type interaction, *F*(1, 30) = 1.741, *p* = 0.184, η_p^2 = 0.055.

There was also a marginally significant 3-way interaction between hemisphere, word type, and group, *F*(2,60) = 2.867, *p* = 0.065, η_p^2 = 0.087. 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, *p* = ns, but a significant effect of group, *F*(1, 30) = 5.142, *p* = 0.027, η_p^2 = 0.114, with the sleep group significantly more likely to identify unseen-lure words as old (M = 0.740, SE = 0.037) compared to the wake group (M = 0.620, SE = 0.037). There was also a significant hemisphere by group interaction, *F*(1, 30) = 4.321, *p* = 0.016, η_p^2 = 0.179. Further post-hoc analysis revealed this interaction came from a non-significant difference in the LH between sleep (M = 0.677, SE = 0.053) and wake groups (M = 0.667, SE = 0.053), *F* < 1, *p* = ns, but a significant difference in the RH between sleep (M = 0.803, SE = 0.053), and wake group (M = 0.573, SE = 0.053), *F*(1, 30)= 8.169, *p* = 0.008, η_p^2 = 0.214, 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* = 0.053, η_p^2 = 0.228, or the wake group, *F*(1, 15) = 2.312, *p* = 0.149, η_p^2 = 0.134.

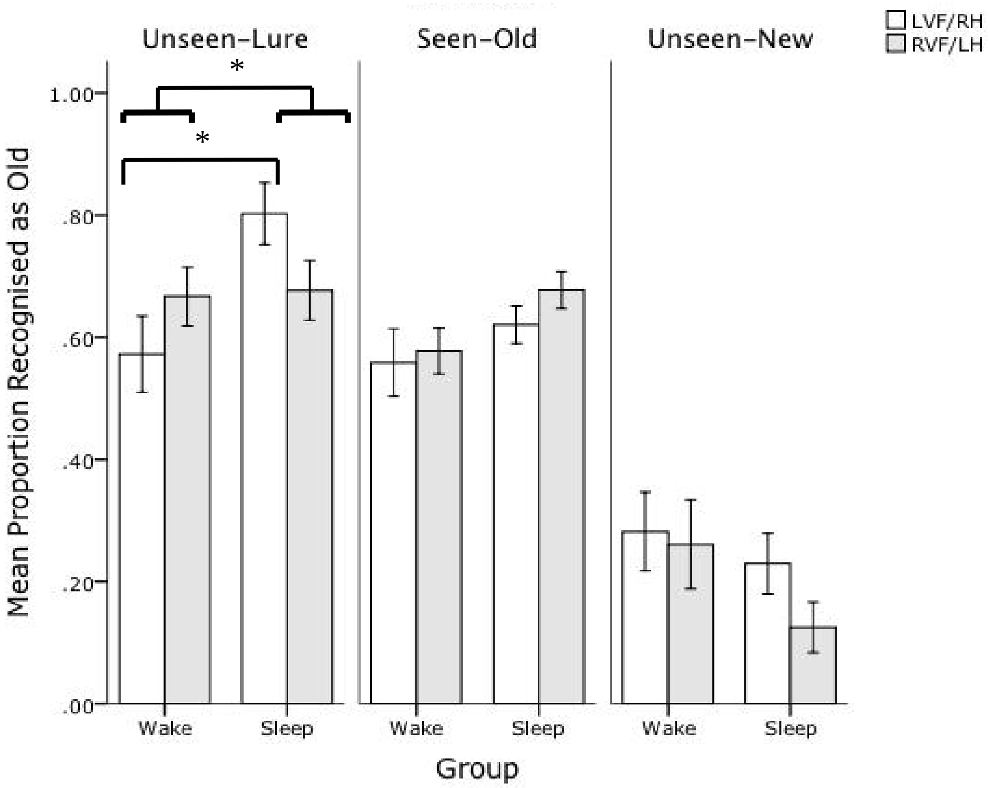

Figure 5.1. Proportion of words endorsed as ‘Old’ by word type for sleep and wake groups by hemisphere. Error bars show ± 1 SEM.

For unseen-new words, as expected there was no significant difference between group, *F*(1, 30) = 1.676, *p* = 0.205, η_p^2 = 0.053, hemisphere, *F*(1, 30) = 2.567, *p* = 0.120, η_p^2 = 0.079, or a group by hemisphere interaction, *F* < 1, *p* = ns. For seen-old words there was no significant effect of group, *F*(1, 30) = 3.433, *p* = 0.078, η_p^2 = 0.100, hemisphere, *F*(1, 30) = 1.201, *p* = 0.282, η_p^2 = 0.038 or a group by hemisphere interaction, both *F* < 1, *p* = ns.

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 5.2). 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 5.3). Correlations between total sleep time and memory accuracy measures were similar.

Table 5.2. 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 ± 0.65
Average Wake after Sleep Onset	17.9 ± 2.08
Average Sleep Onset Latency	12.53 ± 2.03

Table 5.3. 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	-0.121	-0.141	0.151	0.019	-0.173
Stage 2	-0.216	-0.149	-0.029	-0.083	-0.242
SWS	0.083	0.290	-0.162	-0.066	0.285

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, $r = -0.748$, $p = 0.004$ (corrected), see Figure 5.2 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, $r = -0.593$, $p = 0.015$, ($p = 0.045$ corrected), but not between C3-C4 stage 2 spindle density and RH unseen-lure recognition accuracy, r = -0.471, $p = 0.066$, uncorrected), though in each case the lateralisation effects were similar: greater RH compared to LH spindle density resulted in greater false memories.

For F3-F4 stage 2 sleep spindle density, there was no significant correlation between unseen-lure recognition accuracy and F3-F4, $r = -0.066$, $p = 0.808$, nor for LH unseen-lure recognition accuracy, $r = -0.153$, $p = 0.572$, or RH unseen-lure recognition accuracy, $r = 0.009$, $p = 0.973$, with F3-F4.

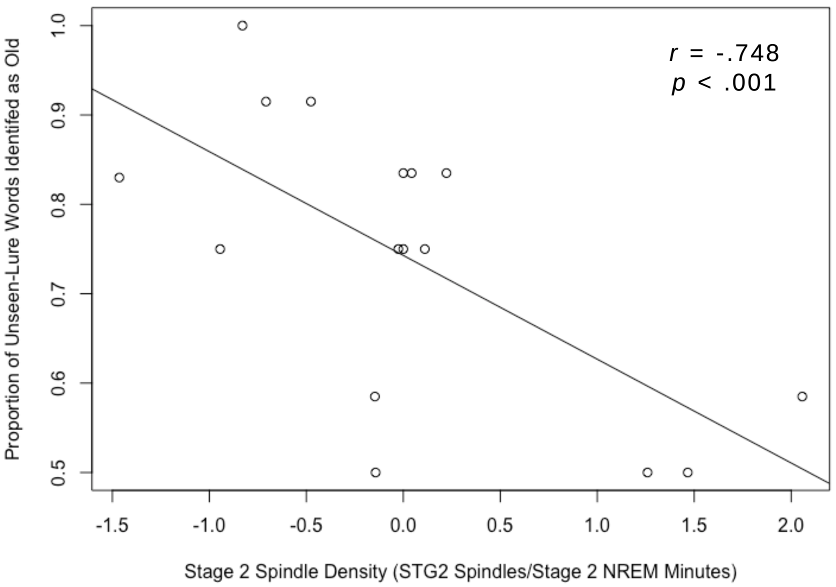

Figure 5.2. Correlation between lateralised spindle density (C3-C4) by unseen-lure recognition accuracy.

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 5.4). 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 5.4). 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 5.4. 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	-0.477	-0.561*	0.012
C4	-0.083	-0.262	0.283
F3	-0.417	-0.204	-0.168
F4	-0.334	-0.082	-0.159

* *p* = 0.024 uncorrected, *p* = 0.288 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 5.5). Hence, the correlations with sleep spindles were only found for the significant behavioural changes in memory performance.

Table 5.5. 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 Recognition
C3-C4	-0.343	-0.067
F3-F4	0.222	-0.162

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 $r < 0.321$, $p > 0.226$. 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 $r < 0.372$, $p > 0.156$.

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* = -0.198, *p* = 0.463, LH unseen lure recognition accuracy, *r* = 0.038, *p* = 0.888, or RH unseen lure recognition accuracy, *r* = -0.273, *p* = 0.306. However, for fast spindles, there was a significant correlation between C3-C4 and overall unseen-lure recognition accuracy, *r* = -0.619, *p* = 0.011, but no significant correlation with LH unseen lure recognition accuracy, *r* = -0.446, *p* = 0.083, or RH unseen lure recognition accuracy, *r* = -0.469, *p* = 0.067. 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 5.6 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 5.6. 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’	0.784	0.862	0.816	0.797
	(0.025)	(0.027)	(0.025)	(0.027)
False Recognition A’	0.867	0.849	0.779	0.841
	(0.029)	(0.028)	(0.029)	(0.028)
True Recognition B’’	0.263	0.574	0.368	0.348
	(0.107)	(0.139)	(0.107)	(0.139)
False Recognition B’’	-0.215	0.463	0.268	0.194
	(0.163)	(0.160)	(0.163)	(0.160)

For A’, there was a significant 3-way interaction between group, hemisphere, and true or false recognition memory, $F(1, 30) = 17.353$, $p < 0.001$, $\eta_p^2 = 0.366$. When split by group, in the sleep group there was a significant interaction between hemisphere and memory type, $F(1, 15) = 10.859$, $p = 0.005$, $\eta_p^2 = 0.420$. 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, $F(1, 15) = 9.930$, $p = 0.007$, $\eta_p^2 = 0.398$, but no difference within the LH, $F < 1$, p = ns. For the wake group, there was again a significant hemisphere by memory type interaction, $F(1, 15) = 6.868$, $p = 0.019$, $\eta_p^2 = 0.314$. Post hoc analysis demonstrated that true recognition was lower in discriminability than false recognition in the LH, $F(1, 15) = 4.895$, $p = 0.043$, $\eta_p^2 = 0.246$, but no difference in the RH, F(1, 15) = 1.539, $p = 0.234$, $\eta_p^2 = 0.093$. 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, $F(1, 30) = 4.571$, $p = 0.041$, $\eta_p^2 = 0.132$. When split by group, for the sleep group there was a memory type by hemisphere interaction, $F(1, 15) = 5.161$, $p = 0.038$, $\eta_p^2 = 0.256$. Post hoc analyses demonstrated that judgments were more conservative for true than false recognition in the RH, $F(1, 15) = 10.848$, $p = 0.005$, but no difference in the LH, $F(1, 15) = 1.491$, $p = 0.241$. For the wake group, there was no significant interaction between memory type and hemisphere, $F < 1$, $p =$ ns. These results demonstrated that sleep affected response bias as well as discriminability in the RH, particularly for false recognition.

4. General 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 (for a summary, see. 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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6. General Discussion

The purpose of the thesis was to further understand the processes and factors in formation of bound representations in memory. Previous literature has demonstrated that different item modalities such as actions, objects, locations, and people, are not equally consolidated either in terms of quantity or fidelity (Kersten et al., 2008; Old & Naveh-Benjamin, 2008). Recent literature appears to suggest a role of pre-existing conceptual knowledge as a potential influence in this (Konkle et al., 2010b) but that was specifically focused upon objects. In the current thesis I sought to expand this to see how the different item modalities are consolidated and to further understand the role of both conceptual knowledge and sleep.

6.1 Thesis Summary

Within Paper 1 I first sought to validate the existing literature on the capacity of the Visual Long-Term Memory (VLTM) in order to establish a baseline level performance of recognition of specific bound representations. As a large number of studies that report these findings in VLTM have primarily used a mono-cultural sample (usually western participants) and as culture has been previously demonstrated to affect subsequent recognition due to foreground-background effects, I sought to see if the previously reported observations of VLTM were a universal phenomenon or one specific to western cultures. This had two important theoretical contributions, 1) it allowed validation of the results of the previous literature within western samples (Urgolites and Wood, 2013b) but also explore whether the previously reported cultural differences would be replicated in recognition of specific bound representations and as to whether this varied with type of stimuli used (action-scene or object-scene). Within the study participants from either a western (UK) or an East Asian (Malaysia) culture viewed action-scene or object-scene composites before completing a 2-alternative forced-choice recognition task. The results suggest that there is a cultural difference on recognition of object-scene composites but not action-scene composites, providing an important methodological point for subsequent studies; that participant-based factors (in this case culture) can significantly affect consolidation of bound representations.

Building upon that result, the second set of experiments (Chapter 3) was the first set of studies into the role of sleep in this form of associative memory. It was theorised that compared to an equivalent period of wake, action-scene recognition after sleep may have benefitted from preferential consolidation as the previous literature suggests that sleep can have a compensatory effect on more difficult associations (e.g., Sio et al., 2013) while for object-scene recognition sleep may have a beneficial effect on consolidation due to promotion of associations between pre-existing item representations. As with Experiment 1, participants were shown action-scene or object-scene composites but introduced a delay of 12h between training and testing, with this 12h containing either a period of wake or sleep. Sleep was found to have no significant benefit on action-scene composite recognition, with accuracy levels at chance levels across all groups. However, sleep was found to be beneficial to object-scene composites, with accuracy in the sleep group (67.7%) significantly higher than the wake group (54.4%). I suggest that there are two factors that affect this, complexity of stimuli and prior knowledge supporting encoding and retrieval, with this discussed in more detail in the next section.

The third set of experiments (Chapter 4) sought to apply the previous results to a more practical situation, that of eyewitness testimony, as the existing literature has revealed that within eyewitness testimony participants are susceptible to errors of binding at retrieval. Adopting the same sleep/wake design as the previous study participants saw 6 videos of various crimes then completed a free recall task as a measure of immediate memory. In the second session participants completed a second free recall task without viewing any videos and retrieved information of actions/objects/people/locations were scored and compared. It was hypothesised that sleep should lead to a larger number of retrieved information compared to an equivalent period of wake, and that in line with the previous literature actions would be recalled to the highest degree compared to the other item modalities (Old & Naveh-Benjamin, 2008). Across the two sessions it was observed a significant difference in details recalled according to item modality, with action details recalled to a higher level than object, location, and people details but there was no observable effect of sleep/wake.

Finally, the fourth experiment (Chapter 5) moved away from visual memory and instead focused on the role of sleep on memory distortion using the DRM paradigm. Previous literature had identified a hemispheric difference in recognition of old/new/lure words in the DRM paradigm after sleep (Monaghan et al., 2016) but as the study used actigraphy, it was unclear what sleep architecture supported this difference. Experiment 4 sought to further clarify this. In the study participants were trained on 12 DRM wordlists and then were assigned either to a wake group or a nap group monitored with polysomnography. At retrieval, participants were presented with old-seen words, new-unseen words, or lure-unseen words, with the latter being semantically related to the old-seen words. Sleep significantly increased lure-unseen acceptance compared to the equivalent period of wake, providing evidence of sleep promoting false memory generation in line with previous studies (Diekelmann et al., 2010; Monaghan et al., 2016; Pardilla-Delgado & Payne, 2017; Payne et al., 2009). Furthermore, RH spindle generation relative to LH spindle generation was significantly correlated with false recognition of lure-unseen words, suggesting a central role of the RH in false memory generation. In the following sections I will explore the results of each study in more detail by looking at the results over the groups of experiments rather than at an experiment-level.

6.2 Different Effects of Modality Within Visual Long-Term Memory

Summary of Chapter 2-4.

The primary focus of chapters 2-4 was to further understand the differences in consolidation between item modalities within the VLTM. The previous literature has observed that the VLTM has a large and detailed storage capacity for individual items. In a seminal paper, Standing (1973) observed that participants could correctly recognise about 6600 images out of 10000 seen, whereas more recent elaborations on this have demonstrated that humans can also store high-fidelity representations of items, with Brady et al. (2008) observing participants could accurately recognise a previous seen item 93% of the time in a 2AFC task, a more challenging task than Standing's due to it requiring specific recognition of the target item as opposed to Standing's study whereby familiarity would be sufficient for a recognition judgement. Moreover, this effect of extensive memory capacity isn't limited to objects, but also scenery (Konkle et al., 2010a, 2010b) and actions (Urgolites & Wood, 2013a), demonstrating that the VLTM is not just capable of storing many items, but also capable of storing them to a relatively high-fidelity. Yet relational memory between the elements is more challenging, with Urgolites and Wood (2013b) demonstrating that although participants could accurately recognize individual items, they could not recognize specific pairs. Urgolites and Wood (2013b) suggested that this was an issue of relational binding in multi-item events. As such the purpose of chapter 2-4 was to further understand the issue of relational binding within multi-item events.

In chapter 2 it was demonstrated that there was a significant cultural difference in recognition of specific multi-item events. The literature surrounding the effect of culture on visual memory is rather contradictory. Early studies in the field, such as Masuda and Nisbett (2001) and Kitayama et al. (2003) suggest that cultural differences in perception of the self as individualist or collectivist can extend to perception of the world with Western cultures engage in analytical processing, attending to each item individually, whereas East Asian culture engage in holistic processing, attending to items within the context and noting relationships between them. However, subsequent studies have demonstrated mixed findings regarding eye movements (Chua et al., 2005, Evans et al., 2009; Rayner et al., 2007). One study of note is that of Millar et al. (2013) who observed that when presented with object-scene composites, Western participants were significantly more accurate in recognising specific items and backgrounds than East Asian participants, who were more likely to falsely recognise similar items as previously seen, suggesting that for East Asian participants, item recognition was promoted at a categorical level rather than at a specific item or item-exemplar level.

Regarding the results of Chapter 2, it was observed that there was no significant difference between Western and East Asian cultures in recognition of action-scene composites, with proportion of items correctly identified across both groups similar to that observed in Urgolites and Wood (2013b). instead, there was a significant cultural difference of object-scene composite recognition, with the Western culture significantly more accurate than the East Asian culture.

Focusing on the cultural factor first, the result can fit in with theories of culture and of visual processing. If, as suggested, East Asian cultures *do* engage in holistic processing (Masuda & Nisbett, 2003), focusing on the relationships between all elements then this may lead to issues regarding attentional splitting, suggesting that any mental representation may be a more generalised, low-fidelity representation of the image and as such more susceptible to a) decay over a period of time, and b) more susceptible to interference from the foil option in the 2AFC task. In contrast, by engaging in analytical processing Western participants were able to benefit in two key ways, a) By focusing on each individual item they could encode a high-fidelity representation of the item aided by prior categorical knowledge (Discussed in the following section, Konkle et al., 2010b) that expedited the encoding process and b) allowed them to focus on the relationship between the two items exclusively. However, future research is needed to understand how generalisable the result is as within the culture paper although we demonstrated a significant difference between Western and East Asian cultures, consistent with the existing literature, the participant samples we used are not typical of the literature. In previous cultural studies participants were usually taken from America and Japan as examples of their respective cultures, whereas in Chapter 2 participants were from the UK and Malaysia. Although this differs from the previous literature, this was by design. While there is little difference between US and the UK in measures of cultural identity, with both defined as individualist (Hofstede, 1983), Malaysia is unique amongst East Asian cultures as while it is considered an East Asian culture, it is one of the few to primarily use the Latin alphabet. For the present task this was an important distinction to make as any pictographic language (e.g., Japanese or Chinese) may have led to a confounding effect (Bagley et al., 1983; Kühnen et al., 2001). Though it is useful in the presented study, it does make it more difficult to extend the results to a wider East Asian population. In order to make such claims it would be important to replicate the study with East Asian cultures that utilise a pictographic language to see if any form of pictographic language would benefit consolidation of bound representations.

6.2.1 Differences in Consolidation by Item Modalities

A consistent result across all studies was that when presented in combinations, the different item modalities were not retrieved to equal levels. In the specific recognition composite tasks in Chapters 2 and 3, object-scene composites were more accurately recognised than action-scene composites, while in the free recall task of Chapter 4, this pattern reversed, actions were recalled more than any other information type. Focusing on the free recall task from Chapter 4 first, the result appears consistent with the current literature; within studies of eyewitness testimony actions are typically reported more frequently than people details, with this occurring in both recognition (Kersten et al., 2008; Old & Naveh-Benjamin, 2008), and recall tasks (Tollestrup et al., 1994). One study, Yuille and Cutshall (1984), noted that free recall of an event typically resulted in actions being mentioned the most (56%), then person details (26%) while objects the least (17%) and that this interacted with accuracy; participants were most accurate for objects (87%), then actions (82%), then people (74%). While the current experiment did not measure incorrect details the distribution of item modalities was similar across all sessions and conditions to the previous literature. The most logical reason for this spread may reflect the type of information that is most salient in the video (Akehurst et al., 2003); for example, the reason actions are typically reported more than objects or people are that people often perform multiple actions, increasing the number relative to other modalities where only one object may be present in the scene. Admittedly, while this is not a major contribution to the literature it provides further evidence of some form of difference in consolidation.

6.2.2 Differences in Specific Composite Recognition: An Action / Object Distinction

The interesting and novel result of both Chapters 2 and 3 is that of object-scene being significantly more accurate than action-scene in specific composite recognition, the first study to demonstrate this effect. This result was, by my own admission, unexpected, with the degree of the difference quite striking. In tests of immediate recognition in Chapter 2 and Chapter 3 (Experiment 1b, 3b) proportion of items correctly recognised for specific action-scene composite averaged approximately 56%, which while significantly above chance suggests that there are issues with bound representations for action and scenes, with these appearing to be more difficult to form into a bound representation of sufficient fidelity for later retrieval. In contrast, object-scene proportion of items correctly recognised in immediate recognition tasks averaged close to 71% in both sets of studies.

To my knowledge, only one study has examined specific action-scene composite recognition in the same manner as those presented here, that of Urgolites and Wood (2013b). Within their study participants were presented with action-scene composite pairs and in subsequent recognition task were presented with the target item and a novel foil and were requested to identify which composite had been previously seen (a 2AFC task). Proportion of items correctly recognised for action-scene composites was close to chance, averaging about 58% suggesting that participants could maintain this association between the two elements but it was fragile, with the results presented in the studies in the thesis consistent with their result. The result proved more complex when proportion of items correctly recognised for the individual elements of the composite (recognition of just the action or just the scene) were close to previously reported levels, implying that participants were able to store high-fidelity representations, the issue was forming the association. Urgolites and Wood's explanation for this difference was primarily neurophysiological. Within the literature there is evidence that action and scene representations are stored separately in disparate locations (the premotor cortex and the medial temporal lobe respectively; see Kravitz et al., 2011) and Urgolites and Wood suggested that the difficulty in binding action-scene was due to this.

Yet the results of the object-scene studies appear to somewhat contradict this theory. As previously said, the object-scene recognition was significantly higher than action-scene, but objects and scenes are also stored separately from one another (prefrontal cortex and medial temporal lobe; Kravitz et al., 2011). As such, there must be another factor to account for this difference. Within the literature it appears that there are three possible factors that may influence the result: the amount of time available for encoding; conceptual knowledge; and semantic labelling as a factor. In the following section I will address each of these explanations and discuss its suitability for explaining the result.

One factor that can be dismissed is encoding time. While object recognition is fast, with brain responses associated with visual discrimination of objects occurring around 150ms (Allison et al., 1999; Thorpe et al., 1996), action recognition within the current study is not possible until 500ms (where the action reaches maximum deviation from the neutral standing position, making what action it is clearest) yet this did not appear to affect the results. Accuracy for the repeat detection task in the training phase was consistently high across all experiments regardless of stimuli type, averaging over 90% with no significant difference between exposure for 1 second and exposure for 3 seconds. Given that the same background-scene stimuli were used for both action-/object-scene composites, it suggests that any difference in recognition is due to the foreground item but not due to differences in distinctiveness or temporal encoding of the stimuli.

When excluding the temporal factor the key difference between objects and actions can be interpreted as differentially accessing pre-existing conceptual knowledge (otherwise referred to semantic memory). Within this context, conceptual knowledge is what Konkle et al. (2010b) refer to as a “conceptual hook”. This refers to a conceptual “item prototype”, a representation of the item that has been formed through multiple exposures and serves as a generalisable point of reference. The objects used in the studies were objects that were highly familiar to participants (e.g., in the food category- Apple, Banana, Cherry). As demonstrated in Chapter 2, familiarity was general across cultures: participants in the East Asian and the Western cultures both reported high familiarity across all items. Within item recognition in the VLTM previous literature has observed that having an item prototype representation can be beneficial in early encoding of object (Brady et al., 2008; Konkle et al., 2010b), allowing expedited encoding of the object as participants do not have to encode the whole item to high-fidelity as they can rely upon the prototype to create a representation of the object within episodic memory. For the actions this was not possible, all actions within the study were novel to the participants and for each category (bend, crouch, jump, and turns) the inclusion of 10 exemplars meant that each action had some degree of similarity to other category members. In having no pre-existing conceptual knowledge of the action, participants were required to create a high-fidelity representation of the item at encoding, a more cognitively demanding task. This effect would not be elicited in the repeat detection task where participants typically score close to ceiling as within that task participants only have to judge whether they had seen the action-scene bound representation before, with participants able to make a judgement based on either familiarity or even just the background.

Furthermore, the link to conceptual knowledge may even extend to semantic labelling. Wiseman and Neisser (1974) observed that when presented with ambiguous faces participants were more accurate in a recognition task for items that they had explicitly labelled as a face, suggesting that labelling is important for visual recognition. This effect has since been extended by Koutstaal et al. (2003) who examined the role of semantic labelling in object recognition. Within their Experiment 1 participants were more accurate in recognition judgements for ambiguous shapes that had been provided with a semantic label than items that were unlabelled. More relevant to the results observed in this thesis, recognition of unlabelled real-world objects was significantly higher than highly distinct, novel items, suggesting that conceptual knowledge is important for item recognition. Thus, it may be that because the objects and scenes already have pre-existing semantic labels, this benefits consolidation as the representation is no longer purely visual but also part semantic; participants no longer have to remember the precise details of the banana on the beach, only the semantic pairing of banana-beach. There is an issue with this suggestion though- it fails to take into account the observed result of Urgolites and Wood (2013b) that even though recognition of composite pairs was relatively low, recognition of individual items was consistent with the previous literature (Brady et al., 2008;

Konkle et al., 2010a, Urgolites & Wood, 2013a). As such, there must be a second factor in why object-scenes were significantly more accurate than action-scenes.

A more compatible explanation may be due to the various functions of the hippocampus in episodic memory. To briefly summarise, the hippocampus is thought to have three primary roles in episodic memory, rapid learning of associations; formation of distinct representations of overlapping stimuli (pattern separation); and retrieval of a complete representation in response to a partial cue (pattern completion). Addressing the functions in order, the hippocampus' role in rapid learning of new associations has been demonstrated in multiple studies (See Horner & Doeller, 2017). fMRI studies have demonstrated that hippocampal 'concept cells', fire in the presence of stimuli related to conceptual knowledge, such as celebrities, animals, or famous buildings (Quiroga et al., 2005; Kreiman et al., 2000), allowing rapid encoding of visual information. Furthermore, concept cells can attune rapidly with literature observing that it can form within hours (Monaco et al., 2014; Quiroga et al., 2009), suggesting that conceptual knowledge is a pivotal factor in rapid consolidation of learned associations.

This function is thought to work in tandem with pattern separation and completion. At encoding, pattern separation allows distinct, non-overlapping representations of information taken from overlapping input. Although the early literature focused on simple stimuli (Bakker et al., 2008), more recent studies have demonstrated that even in complex, multi-item events participants are capable of forming distinct representations for each stimulus (Chadwick et al., 2010). At retrieval pattern completion allows retrieval of the bound representation through cued retrieval of one element by presentation of another, a form of pattern recognition. Horner et al. (2015) observed that participants who had learned person-location-object associations could accurately retrieve both person and object details at retrieval. However, the important result in relation to the current results was that cueing with location led to reinstatement of just the category, not the exemplar-level item, consistent with evidence for reinstatement at retrieval of stimuli categories and low-level visual properties (Bosch, Jehee, Fernandez, & Doeller, 2014; Jafarpour, Fuentemilla, Horner, Penny, & Duzel, 2014; Polyn, Natu, Cohen, & Norman, 2005; Wheeler, Peterson, & Buckner, 2000; Woodruff, Johnson, Uncapher, & Rugg, 2005).

Thus, the difference observed between action-scene and object-scene recognition may be one of the role of conceptual categories in pattern recognition and completion. Objects, by virtue of conceptual knowledge and item prototypes, are initially able to be encoded to a high fidelity representation facilitated by the item prototype from conceptual knowledge. At retrieval, because the objects are to an exemplar-category level (rather than the overall category of fruit, the stimuli consisted of exemplar-categories, e.g., apple), retrieval is expedited as participants do not need to retrieve the high-fidelity representation, just the exemplar-category level item that would be sufficient for recognition judgements of the bound representation (e.g., a typical apple was alongside a typical beach). As actions can only benefit from a more generalised categorical representation (e.g., a jump with a 90º twist to the left may only be retrieved as a jump), retrieval of the specific association is much harder due to the interference of the foil representation offering competing information at a category level (e.g., a jump with a 90º twist to the right). The natural progression of this line of research would be to employ exemplar-level object stimuli, so instead of presenting a ‘food’ category, instead present an ‘apple’ category but with 10 exemplar-level apples. If it is a form of conceptual knowledge benefitting consolidation through distinct item prototypes this may eliminate this factor as the item prototypes for these items would be more distinct. This point is returned to in the future directions section.

6.2.3 Role of Sleep in Consolidation of VLTM Based Bound Representations

The second major contribution from this thesis was that the results of Chapter 3 demonstrated that sleep can aid consolidation of the object-scene pairing compared to an equivalent period of wake but this was not seen in the action-scene pairing, with performance after 12h at chance level for both the sleep and wake group- the first study to do so in this controlled comparison. The result adds to a growing literature on the role of sleep in consolidation of learned associations as previously sleep has been demonstrated to aid consolidation of episodic memory in item-context tasks (van der Helm et al., 2011), related and unrelated word pairs (Gais & Born, 2004), and face-location associative pairs (Ruch et al., 2012). Much previous research has observed that sleep primarily benefits the contextual elements of episodic memory. For example, van der Helm et al. (2011) noted that although word recognition did not differ between a nap and no-nap group, the nap group were significantly better memory for the poster associated with the word (See Chatburn et al., 2014 for a summary on sleep's role in associative memory).

As such, the beneficial effect of sleep on consolidation of the object-scene pairs may be due to sleep's beneficial role on contextual consolidation and hippocampal reactivation during sleep. Within the active systems consolidation model of sleep, during SWS there is additional interaction between the hippocampus and the neocortical sites, with hippocampal firing observed during this period (Bergmann et al., 2012; Peigneux et al., 2004; Wilson & McNaughton, 1994). These hippocampal reactivations aid consolidation of the representations to the neocortical and striatal sites. This additional hippocampal activation acts to further bind the separate item representations, forming a stronger association between the two and reducing the effect of any interference (Ellenbogen et al., 2006). Future studies should use polysomnography to determine the sleep architecture associated with the memory binding effects and see if there is a link between sleep architecture and consolidation.

The second benefit of sleep may relate to the previously observed benefit of prior knowledge promoting rapid consolidation of new information. Recently, Hennies et al. (2016) observed that information that relates to prior knowledge is not only remembered better but is also consolidated more rapidly than information that is irrelevant, with Hennies and Colleagues also linking spindle density to this effect. The study is the latest in a large literature on the role of assimilation of information into conceptual knowledge, with evidence of rapid consolidation observed in both rodents (Tse et al., 2007) and humans (van Kesteren et al., 2010, 2012, 2013, 2014). Recent models of sleep consolidation, such as Stickgold and Walker's (2013) Memory Triage model or Lewis and Durrant's (2011) information Overlap to Abstract (iOtA) model emphasise that pre-existing schemas are the basis for this rapid consolidation. For example, in the iOtA model if the hippocampal reactivation shares overlapping elements with the neocortical representation it can lead to a greater interaction between the neocortical and hippocampal structures, leading to a quicker assimilation process. It may be that the fact that as the object-scene composites had pre-existing conceptual knowledge for both elements this led to greater hippocampal-neocortical interaction, resulting in a strengthened object-scene bound representation. One way to examine this further would be to try and replicate the current study with the stimuli alongside novel, unseen objects. If it is really a factor of pre-existing conceptual knowledge then there should be an observable difference between familiar object-scene composite recognition (e.g., banana-beach) and novel object-scene composite recognition (*blicket*-beach).

The difference between action-scene and object-scene recognition and the role of sleep may further reflect the impact of conceptual knowledge on forming associations. Sleep was able to have a beneficial effect on the object-scene bound representations due to the initial association of object-scene being strong enough to survive a delay from encoding to sleep while the action-scene association, although able to be encoded as a bound representation (as seen in the immediate testing task), was already fragile and thus, did not survive the delay to recognition testing.

6.2.4 The Role of Sleep in False Memory Generation

Within the final study (Chapter 5), it was observed that RH sleep spindles *relative* to LH sleep spindles significantly correlated with false memory generation; the greater the RH spindles relative to LH spindles, the greater the false recognition. The result adds to a growing literature on the role of sleep on false memory generation. In summary, the previous false memory literature has been relatively contradictory; while some studies have demonstrated that sleep can increase false memories (Diekelmann et al., 2010; Pardilla-Delgado & Payne, 2017; Payne et al., 2009), others have observed no effect of sleep (Diekelmann et al., 2008), or even a reduction in false memories (Fenn et al., 2009). Part of the reason for this difference is the type of task used, false recall typically elicits a sleep-based false memory effect, but recognition doesn't (See Chatburn et al., 2014; Pardilla-Delgado & Payne, 2017), with this difference partly due to recognition task acting as additional source-monitoring, cueing memory

Why was the study able to demonstrate a sleep-based false memory effect in recognition when previous studies (e.g., Fenn et al., 2009; Pardilla-Delgado & Payne, 2017) could not? I suggest the key difference lies in the recognition task itself, employing a hemispheric recognition task ensures processing is located within one hemisphere and allowed us to observe differences in semantic networks. As covered in the literature review, one of the suggested functions that occurs within the hippocampus is that of pattern recognition and completion; after initial encoding humans are able to “fill in the blanks” and complete the pattern using conceptual knowledge. In the case of hemispheres, this may explain the hemispheric difference in false recognition and links nicely to established models of hemispheric semantic processing. The dominance of the LH over the RH in word processing is well established (for a summary, see Hellige, Laeng, & Michimata, 2010), theorised to occur in part due to the LH containing the long-term vocabulary store (Ellis et al., 2009). This hemispheric bias has been observed within the false memory literature (Bellamy & Shillcock, 2007; Ito, 2001; Westerberg & Marsolek, 2003) with the RH being more susceptible for false recognition than the LH, suggesting that at least for processing of stimuli in the DRM paradigm there is some form of hemispheric division of labour. Prominent theories for this effect is the difference in hemispheric language processing as proposed by Beeman's (1998) coarse and fine coding theory; the RH processes input in a coarse manner, weakly activating many associated words while the LH processes in a fine manner, strongly activated a few associated words. When combined with hemispheric-based hippocampal pattern completion this would mean that words being presented to the RH at testing prompt retrieval from the broad semantic network, thus making it more likely to falsely recognise a critical lure. It is this form of prompting specific semantic networks that can explain the difference between the current study and those previous findings with regard to sleep and false memory recognition. In standard recognition tasks (whereby the word is presented centrally and until a judgement is made, e.g., Fenn et al., 2009), the dominance of the LH in facilitating word processing would override any form of RH activation, thus any false recognition within the RH would be masked by the LH correctly making a judgement. It is only in presenting words to specific hemispheres that the effect can be elicited.

6.2.5 Sleep Architecture in False Memory Generation

One of the aims of the nap study (Chapter 5) was to determine the sleep associated mechanisms in false memory generation. While previous studies on false memory generation have found links between SWS and false memories (Payne et al., 2009) none had looked at the role of spindles in false memories, despite a large literature demonstrating that spindles are strongly correlated with consolidation of associative memory.

First, I wish to address the lack of finding of the previously observed correlation between SWS and false memory generation (Payne et al., 2009). Within the nap study there were no significant correlations between any measure of sleep stage and consolidation yet this is not that much of an issue when considered within the wider literature. At the time of writing, only two studies have examined sleep stages and false memory, that of Payne et al. (2009) and Pardilla-Delgado and Payne (2017). Within the former, Payne et al. observed a significant negative correlation between SWS and accurate recall, suggesting that SWS promoted a gist-based consolidation of memory, consistent with contemporary theories of sleep-based consolidation (Lewis & Durrant, 2011; Stickgold & Walker, 2013). However, Pardilla-Delgado and Payne were unable to replicate this, observing no significant correlation between SWS and accurate recall, but instead observed a *negative* correlation between SWS and false recognition, but this was only apparent for low performers (participants whose performance fell below a median split for true recall).

Why was our result different? There are numerous possible factors ranging from study design and type of data analysis. Beginning with the methodology, although the study in Chapter 5 and the Pardilla-Delgado and Payne (2017) paper use a recognition paradigm, Pardilla-Delgado and Payne presented a free recall task *before* the recognition task, with this previously demonstrated to act as a potential confound (Roediger & McDermott, 1995). Staying with methodology, the current study used a nap paradigm while Pardilla-Delgado and Payne's used a overnight/48hr paradigm, again this can lead to qualitatively different results. Although data analysis was consistent across both papers (non-parametric *A'*), Pardilla-Delgado and Payne only found the significant correlation between SWS and false memory generation is low performance participants (those whose accuracy fell below the group mean) and as this form of distinction was not made in the Chapter 5 paper this too may have led to the differences in results. As such, it may be that the correlation between SWS and false memories is one that is too fragile to reliably replicate when changes are made.

Despite the lack of any correlation between sleep stages and false memories, there was a significant correlation between sleep spindles and false memories- the greater the spindle density in the RH relative to the LH, the greater the false recognition. The result adds to a growing literature on the role of sleep spindles in consolidation. Past research has linked spindles to a number of cognitive features, including IQ (Nader & Smith, 2001; Schabus et al., 2004), and performance in both procedural (Meier-koll et al., 1999; Fogel & Smith, 2006; Fogel et al., 2007; Nishida & Walker, 2007; Tamaki et al., 2008; 2009) and declarative tasks (Clemens et al., 2005; Gais et al., 2002; Ruch et al., 2012; Tamminen et al., 2010, 2013; van der Helm et al., 2011), but this is the first study to link spindle density to false memory generation. The result is consistent with a recent study by Hennies et al. (2016) who observed that spindle density was linked to prior knowledge. Within their study Hennies et al. established a schema for participants and then presented facts that were either schema-consistent or schema-unrelated. After a period of sleep it was observed that sleep spindle density predicted an increase of the scheme benefit to memory across the interval, with spindle density associated with reduced decay of schema-consistent memories.

When applied to the current study it may be that the link between spindle density and false recognition may reflect a similar mechanism of prior knowledge benefit. As the DRM paradigm relies upon pre-existing semantic associations in order to elicit false recognition, much like the link between schema-consistent information and spindle density the same mechanism may be in effect here. This theory may also explain why the increase in false recognition was linked to hemispheric-based spindle density; an increase in RH spindles compared to LH spindles resulted in greater false recognition. The observation of a hemispheric bias in spindle activity is not novel in itself; In a procedural task Nishida and Walker (2007) found that spindles in the RH related to performance. Within associative memory, van der Helm et al. (2011) noted that S2 fast spindles at C3 strongly correlated with context-memory retention after sleep. Perhaps most pertinent to the nap study is that of Tamminen et al. (2010) who demonstrated that consolidation of novel words into existing semantic networks correlated with LH sleep spindles. Tamminen et al. suggested that this LH spindle bias was in part due to consolidation of vocabulary being lateralised to the LH, the proposed site of the long-term vocabulary store (Ellis 2004, 2009). As discussed in the above section on hemispheric false recognition, the RH is theorised to be more susceptible to DRM based false recognition due to it processing language within a broad semantic network, weakly activating many associative words rather than a few strongly associated words (Bellamy & Shillcock, 2007; Ito, 2001; Westerberg & Marsolek, 2003), with the RH akin to a schema. Therefore, much like the Hennies et al. (2016) study spindle density in the RH may reflect a similar process of schema/gist consolidation within a semantic network. In situations whereby the spindle density within the RH is greater than the LH, thus greater consolidation of a gist form of semantic consolidation, this would reflect in greater false recognition. In contrast, when the LH is more dominant, this would reflect consolidation within semantic networks that only activate a few closely associated words, reducing the chance of false recognition.

6.3 Methodological Limitations

Although each chapter addresses methodological limitations individually for each study, it is worth highlighting the more global limitations. One potential limitation of the experiments involving sleep was the use of the Stanford

Sleepiness Scale (SSS). Although the SSS is widely used in the literature and deemed to be accurate, it is not perfect. Critics of the SSS highlight the judgement required in the SSS (1-7 Likert scale, from Very alert through to Completely exhausted, cannot function efficiently), is not necessarily a measure of sleepiness but rather one of fatigue or boredom levels (Akerstet, Anund, Axelsson, & Kecklund, 2014), and requires participants to be consciously aware of their fatigue levels. Unfortunately, it was only after the completion of all experiments that I learned of the Karloniska Sleepiness Scale (KSS). Advocates of the KSS emphasise it’s a more direct measure of sleepiness, with sleepiness rating on the KSS linked to shift work, jet lag, driving, attention, and it has even been correlated with sleep physiology and behaviour measures (Kaida et al., 2006). As such I’d recommend that if any future work wishes to extend the work within the current thesis it should use the KSS as the measure of sleepiness.

A second limitation was that with the exception of the study in Chapter 5 all sleep studies were ran with actigraphy rather than polysomnography. Although the use of actigraphy as a measure of sleep is prominent within the literature, it lacks the precision of polysomnography that would allow any links between specific sleep stages and the observed results. Given the interesting result of Chapter 3 whereby object-scene recognition was affected by sleep a deeper understanding of the sleep stages and sleep architecture that led to such a result would be beneficial.

Although already highlighted in Chapter 4 it is worth noting again that there was a particular methodological problem with the sleep and item modality study, that of immediate testing. While it is important to gain a measure of immediate recall of information to account for individual differences within the current study it may have hindered what we sought to test. There is a large literature that demonstrates that immediate testing of information can benefit subsequent retrieval even up to a month after initial exposure (Roediger & Karpicke, 2006a, 2006b), as such trying to find an effect of sleep after 12h may have been optimistic at best. In retrospect, the study may have been more complete if it included two more experimental groups who were exposed to the stimuli but did not complete the first recall task until after a delay containing sleep or wake, with a subsequent recall task 24h after the initial exposure. Within this design we could measure the role of sleep/wake on recall within the first recall task but also gain a measure of individual differences in memory.

6.4 Future Directions

6.4.1 Role of Culture- Does a Pictographic Language Help?

One of the key methodological decisions in the Cultural Binding memory paper (Chapter 1) was the decision to test a Malaysian population rather than a more typically researched East Asian population, such as Chinese or Japanese. There were methodological reasons for this. First the study could be run in Malaysia's Sunway University due to a partnership between Sunway and Lancaster. The importance of being able to test in the 'home country' cannot be understated; Previous literature has demonstrated that participants from one culture living in another (e.g., East Asian living in America) can modify perceptual processing to accommodate the new culture relatively quickly (Kitayama et al., 2003), as such in order to get representative data it was important for the data to be collected within the culture. Second, Malaysia's use of the Latin alphabet widespread adoption of English makes it unique across East Asian cultures and a great population to study to account for any potential confound effects of a pictographic language benefitting visual memory (Kühnen et al., 2001). While there was an observable difference between Western and East Asian cultures the natural progression would be to now include one of the East Asian cultures with a pictographic language and see if it influences specific composite recognition.

6.4.2 Binding of Objects and Actions: Why The Gap?

Based on the results of both Chapter 2 and Chapter 3 there is a significant difference in recognition of object-scene composites and action-scene composites. One possible area to explore is to look at the effect of language on this form of task. There’s a large literature that demonstrates that language can play a crucial role in non-verbal cognitive tasks (e.g., Dessaglegn, & Landau, 2008; Spivy, Tyler, Eberhard, & Tanenhaus, 2001, Pyers, Shusterman, Senghas, Spelke, & Emmorey, 2010). Specifically, in VLTM research several studies have demonstrated that memory for visual images is better when images are semantically labelled compared to those that are not (Wiseman & Neisser, 1974; Koustaal et al., 2003; Bower, Karlin, & Dueck, 1975). For example, Wiseman and Neisser noted that in a face recognition task, participants were more accurate in subsequent recognition tasks in images they had judged to be faces, despite all images containing faces to various levels of distortion, suggesting that just being able to label an item can aid recognition. In the thesis the recognition tasks were unequal in this sense- objects already have a label while the actions may not have. Therefore, it may be interesting to see what may happen if modified so that either completely novel objects were used in the object-scene task or that actions were given a label within the task. An alternative design may be to introduce some form of language interference during the task, such as a verbal shadowing task. If language *does* play a role in successful binding then a verbal shadowing task should have a noticeable effect on binding ability.

A second expansion on this could be changing the variance within categories. One of the suggestions in Chapter 3 was that this difference between the two tasks may have been the result of reduced variety across actions within each category compared to objects (e.g., food- banana, cherry, apple, chocolate bar), with Konkle et al. (2010b) previously demonstrating that greater variance within a category can aid encoding/retrieval. If in the object-scene task variance within a category was reduced to a similar level to that of the action-scene task (e.g., rather than a food category, a cup category with similar cups), it may reduce accuracy, allowing a better understanding of what can affect retrieval binding.

6.4.4 Role of Schema in *Visual* False Memories

One study that could bridge the gap between the two areas of the thesis is that of a study on the role of sleep in *visual* false memories. From the Item modality study of Chapter 4 I suggested the result was in part due to gist memory leading to a null result- in recall tasks such as that participants can answer adequately with a gist-based answer, so rather than saying the man punched the victim with a left hook (as may be shown in the action-scene composite task of Chapter 2-3), simply saying the man hit the victim is sufficient.

Although mentioned briefly in Chapter 4, one possible way of exploring this would be similar to the work of Lew and Howe (2016). Within their study participants viewed visual scenes (e.g., a kitchen) that were manipulated for schema-consistent (e.g., frying pan on the cooker top), schema-inconsistent (e.g., plate in the oven), or schema-unrelated (e.g., toilet brush on the cooker). They observed that participants were more likely to falsely recognise the schema-consistent information for the schema-inconsistent stimuli (e.g., for the above example, false recognition of plate on a table), while the schema-unrelated information was highly accurate, due to the item being ‘outside’ of the schema. Given the literature suggesting that sleep can aid integration of information that is schema consistent (e.g., Hennies et al., 2016; Lewis & Durrant, 2011; Stickgold & Walker, 2013), it may be interesting to see if this may extend to visual false memories.

6.4.5 Replicate the Nap Study in an Overnight Paradigm.

Based on the nap study (Chapter 5) the natural progression of the result is to try to replicate the result in an overnight sleep design. Although a result was observed in the nap design overnight sleep is qualitatively different. Within overnight sleep there is an effect of hemispheric lateralisation: the RH compared to the LH is more active during the early half of the night before the LH equalises the activity (Casagrande & Bertini, 2008a, 2008b, Natale et al., 2007; 2010). This is of particular relevance as it is also during this period of RH dominance that SWS is the most prominent before reducing as the night goes on. As Monaghan et al. (2016) observed similar behavioural results (in fact acting as the precursor to the current study), it would be interesting to see if the results would be replicated and extended with measurement of sleep with polysomnography.

6.5 Conclusion

In conclusion, this thesis has provided theoretical contributions within two key domains- the literature on bound representations within episodic memory and the literature on sleep’s role in consolidation. Building upon the results of the chapters I suggest that within bound representations there are two key factors that ultimately affect the memory- participant effects and item effects that interact with each other and affect both encoding and retrieval. Moreover, sleep appears to significantly interact with both of these.

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Appendix 1. DRM Wordlist used in Chapter 5, taken from Stadler et al. (1999)

BREAD: butter, food, eat, sandwich, rye, jam, milk, flour, jelly, dough, crust, slice, wine, loaf, toast

CAR: truck, bus, train, automobile, vehicle, drive, jeep, Ford, race, keys, garage, highway, sedan, van, taxi

CHAIR: table, sit, legs, seat, couch, desk, recliner, sofa, wood, cushion, swivel, stool, sitting, rocking, bench

DOCTOR: nurse, sick, lawyer, medicine, health, hospital, dentist, physician, ill, patient, office, stethoscope, surgeon, clinic, cure

FRUIT: apple, vegetable, orange, kiwi, citrus, ripe, pear, banana, berry, cherry, basket, juice, salad, bowl, cocktail

KING: queen, England, crown, prince, George, dictator, palace, throne, chess, rule, subjects, monarch, royal, leader, reign

MOUNTAIN: hill, valley, climb, summit, top, molehill, peak, plain, glacier, goat, bike, climber, range, steep, ski

MUSIC: note, sound, piano, sing, radio, band, melody, horn, concert, instrument, symphony, jazz, orchestra, art, rhythm

NEEDLE: thread, pin, eye, sewing, sharp, point, prick, thimble, haystack, thorn, hurt, injection, syringe, cloth, knitting

RIVER: water, stream, lake, Mississippi, boat, tide, swim, flow, run, barge, creek, brook, fish, bridge, winding

SLEEP: bed, rest, awake, tired, dream, wake, snooze, blanket, doze, slumber, snore, nap, peace, yawn, drowsy

THIEF: steal, robber, crook, burglar, money, cop, bad, rob, jail, gun, villain, crime, bank, bandit, criminal