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The Effect of Sleep on Memory Consolidation of Emotional and Distinctive Composite Scenes

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An abstract of
A dissertation submitted to the Faculty of the
James T. Laney School of Graduate Studies of Emory University
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Abstract

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Episodic memory for emotionally arousing stimuli is usually enhanced relative to neutral stimuli. However, this enhancement for arousing stimuli is also associated with memory costs to background, neutral information, a phenomenon known as the *emotion-induced memory trade-off effect*. Moreover, it has been established that this memory trade-off increases after a period of sleep, suggesting sleep may selectively enhance emotional memory via consolidation. It has been previously established in the laboratory that distinctive information can also elicit similar memory trade-offs; suggesting that similar cognitive processes may underlie trade-offs for emotional and distinctive information. However it is currently unknown whether distinctive information is also preferentially consolidated after sleep. Therefore, the primary aim of the current research was to extend existing literature examining how emotion influences what information is better remembered by manipulating both affective and non-affective factors (such as distinctiveness) to determine what influences consolidation processes. Memory consolidation was examined by manipulating sleep in two separate studies. Both studies used a memory trade-off paradigm to investigate what information is selectively enhanced after sleep. At encoding, participants viewed scenes consisting of an item (either negative, positive, neutral, or visually distinctive but emotionally neutral) against a neutral background. After an interval, which included a period of sleep, participants completed an incidental recognition test on the items and backgrounds presented separately. In Study 1, consolidation was investigated over the course of a full night of sleep. The goal was to replicate previous findings, which observed enhanced memory trade-offs for negative scenes after sleep relative to neutral scenes, and extend those findings to investigate whether similar enhancements would also be observed for positive and distinctive scenes. In Study 2, the role of sleep in consolidating distinctive, negative and positive composite scenes was further investigated by examining the relation between different components of sleep and memory performance using a polysomnography-recorded nap paradigm. In Study 1 we observed no benefit of sleep on memory performance, but we did observe weak correlations between memory for neutral information and sleep duration, and both deep sleep and REM. In Study 2 we did not observe an enhanced memory trade-off after a nap; however, we did observe a marginally significant sleep-related increase in memory for all items and a significant sleep-related increase in memory for neutral items. Moreover, we observed weak correlations between sleep duration and memory for distinctive items and positive items, time in Stage 2 sleep and memory for negative backgrounds and positive items, and sleep spindle density and memory for negative backgrounds. Overall the findings provide tentative evidence that the beneficial benefits of sleep may be dependent on the experimental context, such as the study paradigm used, and highlight the importance of examining multiple affective factors when investigating the enhancing effects of sleep on memory.

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General Introduction

The ability to remember is central to our lives, and yet it is impossible to remember everything we experience. Remembering absolutely everything would likely exhaust cognitive resources leaving few to engage in other cognitive tasks, and thus impair other forms of cognition, such as insight and creativity. In fact, we do not remember everything we experience, but instead preferentially remember some things over others (Brown & Kulik, 1977; LeDoux, 1993; Singer & Frank, 2009; Wilhelm et al., 2011). One factor that has been shown to influence what information is preferentially remembered is emotion. Indeed, it is well established that emotion is a powerful influence on memory as emotional events are often better remembered than neutral, or everyday, events (McGaugh, 2004).

Emotion is thought to affect memory in a variety of different ways, such as including allocating attention towards salient information during learning (Easterbrook, 1959), and serving as a cue to retrieve and re-experience an emotional event (Buchanan, 2007). Emotion can also affect memory after initial encoding by modulating processes that convert initially labile memories into more enduring memory traces that can withstand the passage of time (McGaugh, 2004). This collection of offline processes, which occur in the hours to days immediately after encoding and enhance memory, are termed *memory consolidation* (McGaugh, 2000) and may occur during sleep (Walker & Stickgold, 2006). The role of sleep in memory consolidation (Diekelmann & Born, 2010; Ellenbogen, Payne, & Stickgold, 2006; Stickgold, 2005), and more specifically in consolidating emotional information (Payne & Kensinger, 2010; Walker & van Der Helm, 2009) is of considerable interest. In this review, I will first discuss affective and non-affective characteristics of emotion which may potentially enhance memory. Then, I will discuss the hypothesis that these aspects may enhance memory through consolidation processes that occur during sleep. This review will also serve as an introduction to two experiments, which will investigate the hypothesis that different affective and non-affective factors of emotion partially enhance memory through sleep-dependent consolidation processes.

Characteristics Of Emotion That Enhance Memory

Emotion influences memory in a variety of ways. Researchers have long observed that individuals can form vivid, highly detailed, and durable memories of surprising, consequential, and emotionally arousing events that they have experienced, such as assassinations of international leaders, a phenomenon referred to as 'flashbulb memories' (Brown & Kulik, 1977). Individuals with post-traumatic disorder (PTSD) will often experience persistent and frightening thoughts and memories of a traumatic ordeal (Brewin, 2001), whereas individuals with depression will often ruminate on negative memories from the past (Hertel, 2004). Emotion is thought to influence memory consolidation, broadly defined as a time-dependent, offline collection of neurobiological processes that converts initially labile and fragile memory representations into a more enduring form (McGaugh, 2000) through a variety of factors.

The two most widely-accepted factors that contribute to memory are arousal (strength or intensity of emotion associated with experience) and valence (how positive or negative an experience is) and they are typically characterized in a two-dimensional space (Kensinger, 2004; Lang, Greenwald, Bradley, & Hamm, 1993; Russell, 1980). In one dimensional view of emotion, the dimension of arousal is described as ranging from calming or soothing to exciting or agitating, whereas the dimension of valence is described as ranging from highly positive to highly negative (Lang, Greenwald, Bradley, & Hamm, 1993; Russell, 1980). Studies investigating the enhancing effects of emotion on episodic memory (memory for experiences or events) typically compare neutral information (i.e., events that are neither highly negative nor highly positive and are not exciting or agitating) with events that are both arousing (i.e., exciting or agitating) and at the extreme end of the valence scale (i.e., highly positive or highly negative). As a result, many of these studies leave unanswered questions about the relative contributions of the valence and arousal dimension to processes which contribute to memory enhancement, such as memory consolidation (Kensinger, 2004).

Much of the support for emotional arousal influencing memory consolidation comes from studies of nonhuman animals (McGaugh & Roozendaal, 2002; McGaugh, 2000, 2004). Emotional arousal is thought to influence memory consolidation in part via upregulation of the hippocampus, a structure critical for memory consolidation, via outputs from the amygdala, a structure whose activity is often increased during the processing of emotionally arousing stimuli (McGaugh, 2004). However, several human neuroimaging studies confirm that the amygdala selectively contributes to the enhancement of emotional but not neutral declarative memories (declarative memory is broadly described as information that can be consciously recalled and is hippocampal-dependent memory) (Cahill et al., 1996; Cahill, Babinsky, Markowitsch, & McGaugh, 1995; Hamann, Ely, Grafton, & Kilts, 1999). In addition, it has been demonstrated that when emotional arousal is equated between positive and negative pictures, subsequent recollection performance is enhanced to an equivalent degree (Anderson, Wais, & Gabrieli, 2006).

With respect to the other dimension of emotion, valence, the evidence for memory enhancement is less clear. Although it is established that memory performance could differ for positive and negative information for various reasons, most studies implicate encoding (the initial formation of a memory representation) processes (Kensinger, 2004; Ochsner, 2000). Some evidence suggests attentional and perceptual biases (e.g., threat, weapons focus) are commonly found for negative but not for positive stimuli, leading to a narrowing of attention for the most salient (i.e., negative) items in a scene (Christianson & Fällman, 1990). Much of the evidence for memory enhancements as a result of valence implicates strategic encoding processes such as elaboration (Kensinger, 2004). Elaboration broadly refers to the process of intentionally establishing links between newly encountered information and previously stored information (Craik & Lockhart, 1972). It has been demonstrated that when individuals process items in an elaborative manner (i.e., extracting meaning from items or forming inter-item associations), memory is enhanced (Craik & Tulving, 1975). With respect to emotional information, it has been suggested that individuals are more likely to elaborate on emotionally valenced items because they are more semantically related to each other than to neutral items (Kensinger, 2004). Consistent with this idea, it has been demonstrated that memory enhancement for emotionally valenced items is reduced when memory is compared for semantically related negatively-valenced words and neutral words (Talmi & Moscovitch, 2004). Moreover, memory advantages for negatively valenced words can be eliminated in a divided-attention task, during which participants attention is divided during encoding preventing elaborative processing (Kensinger & Corkin, 2004). With respect to consolidation, it could be assumed that information that undergoes deeper processing at encoding (i.e., increased elaboration) would be preferentially consolidated (Tucker & Fishbein, 2008). It is important to note, however, that there is currently a paucity of studies investigating the effects of positive emotion on processes like elaboration and consolidation. One reason for this lack of attention may be that brain regions linked with emotional memory, namely the amygdala, are most consistently linked with negative emotion (for review, see Hamann, 2001) thus increasing the focus on the effects of negative emotion on memory. Nevertheless, it has been demonstrated that the amygdala is also implicated in the processing of both positive and negative stimuli (Hamann, Ely, Hoffman, & Kilts, 2002; Hamann & Mao, 2002) and that amygdala activation is correlated with enhanced memory for positive and negative stimuli (Hamann et al., 1999). However, despite sharing similarities in brain regions it is still unclear whether positive and negative information influence memory processes, such as consolidation, through the same mechanism or overlapping ones. As a result, there is an increasing the need for future studies memory studies, which measure the effects of valence on memory consolidation.

Another way in which emotion can influence memory is by increasing the distinctiveness of a scene by increasing attention at encoding, which will lead to increased consolidation and enhanced subsequent memory performance for those distinctive emotional items. Emotional information, however, is typically only described in terms of its two affective dimensions (arousal and valence) and as a result most of the literature discusses the influence of emotion on memory consolidation in terms of affective dimensions (Ochsner, 2000). However, it remains unclear if other factors could account for enhanced memory performance. Specifically, it could be argued that it is not the affective value of emotionally arousing stimuli that make them more distinctive, but rather some other properties that they may share with non-arousing stimuli (for discussion, see Ochsner, 2000). Affective stimuli are typically more unusual, more interesting, more novel, or less expected and it is possible that one or more of these attributes are what makes these stimuli more distinctive.

Some studies have demonstrated that memory performance for distinctive items (i.e., neutral items that are made distinctive by the context in which they are placed), is equivalent to memory for negative emotional items (Mitchell, Livosky, & Mather, 1998; Pickel, 1998), suggesting that factors such as distinctiveness could partially account for enhanced memory performance for emotional stimuli. Moreover, specific brain regions, such as the amygdala, are linked to processing of both emotional and distinctive information (Blackford, Buckholtz, Avery, & Zald, 2010), which suggests a possible overlap in how these different attributes are processed by the brain. However, as was noted above in relation to positive stimuli, it remains unclear whether distinctive information and emotional information are processed through a common mechanism for ‘salient’ information or separate but overlapping mechanisms. Investigating how multiple stimulus attributes such as distinctiveness, valence and arousal modulate memory consolidation would be one potential approach to this question.

Emotional Memory Enhancement Is Selective

Increasing evidence suggests that rather than remembering all aspects of an emotional experience, individuals will actually preferentially remember the most salient elements of an emotional event at the expense of the peripheral background details, a phenomenon that has been termed an *emotion-induced memory trade-off* (Kensinger, Garoff-Eaton, & Schacter, 2007). A predominant theory (Easterbrook, 1959) proposes that as attention is drawn toward emotionally arousing information, fewer attentional resources are left for processing information that is peripheral to the central (e.g., salient) emotional component. This trade-off in attentional resources would be expected to lead to enhanced memory for central emotional information at the expense of background information, because of the well established relationship between increased attention and enhanced episodic memory (Chun & Turk-Browne, 2007; Riggs, McQuiggan, Farb, Anderson, & Ryan, 2011; Talmi, Schimmack, Paterson, & Moscovitch, 2007). Studies evaluating memory for negative vs. neutral scenes support the view that preferential allocation of attention to emotional visual stimuli can enhance memory for the central emotional items at the expense of memory for peripheral scene details (Buchanan & Adolphs, 2002; Kensinger et al., 2007).

Studies examining the emotion-induced memory trade-off effect have typically compared memory for only negatively arousing and neutral stimuli. As a result, unresolved questions remain about the degree to which memories are differentially affected by valence and by non-affective components (i.e., distinctiveness). Examining these additional dimensions would help begin to address whether factors such as valence, arousal, and distinctiveness modulate memory through a common saliency mechanism or through overlapping mechanisms. Waring and Kensinger (2009) investigated the effect of valence on the memory trade-off effect and found that young adults showed a memory trade-off for negative items and not positive items. However, items were not fully matched in terms of arousal (e.g., overall arousal for positive objects was not as high as overall arousal for negative objects). As a result, the differences in memory trade-off effects between negative and positive stimuli, and specifically the lack of a memory trade-off for positive stimuli, may have been a result of the negative items being more arousing, thus decreasing potential influences of positive valence on memory selectivity.

Conflicting evidence also exists regarding the effect of distinctiveness on the memory trade-off. When investigating what factors could account for the phenomenon of *weapon focus* (a memory trade-off where attention is focused exclusively on the weapon in a crime scene, resulting in decreased memory for details of the associated crime), Christianson et al. (1991) found that the distinctiveness of scene details (defined by using a neutral item in an unusual way, such as a person carrying a bicycle over their shoulder) did not result in a trade-off. Although individuals initially overtly attended equally to distinctive and negative central features of a scene, memory improvements were only observed for the negative central features. Mitchell et al (1998), on the other hand, found that scenes depicting a bank robbery with either a negative (e.g., a gun) or novel (e.g., a celery stalk) item (novel in the sense that the item was unexpected in the scene context, which would increase distinctiveness) showed equivalent trade-offs in memory, suggesting that distinctiveness could also play an important factor. Consequently, it remains unclear whether it is the affective components of a scene or some other variable (e.g., distinctiveness), or a combination of these factors that results in enhanced memory for selective components of a scene. One important note regarding the previous studies on distinctiveness is that they tested overall memory for the whole scene and did not separately investigate memory for central salient items and background information, which is how previous studies examining the effects of negative emotion have examined the question (Kensinger et al., 2007). As a result, it is unclear whether distinctiveness influences memory trade-offs in the same way as negative emotion. This unresolved question highlights the need to directly compare the two factors in a memory trade-off paradigm.

It is important to note that despite implicating consolidation in many of the studies mentioned above, none of the previous memory trade-off studies were able to unambiguously isolate consolidation as being responsible for selective memory enhancements. As alluded to earlier, emotion can alter the likelihood that an experience will be encoded and can additionally affect how events are re-experienced at retrieval (processes involved in re-accessing and reconstructing aspects of an encoded memory representation) (Kensinger, 2009). Consequently, it is possible that effects of emotion on encoding and retrieval could lead to memory trade-offs. For example, it is possible that attention preferentially allocated to emotional information will solely account for a memory trade-off and not any subsequent processing during consolidation. Strong evidence for emotion influencing consolidation comes from studies that examine how emotional memories evolve over time. In particular, it has been demonstrated that memory for emotionally arousing information can remain constant or improve over time relative to similar but non-emotional information (LaBar & Phelps, 1998; Sharot & Phelps, 2004). Evidence demonstrating the effects of emotional arousal are magnified after longer (≥24 hours) delays (Sharot & Yonelinas, 2008) suggest that emotion may influence slow, offline memory consolidation processes during sleep (for review, see

Walker & van Der Helm, 2009). However, before describing how emotion may influence sleep-dependent consolidation processes it is first important to define sleep.

Stages of Sleep

Sleep is broadly divided into two separate sleep stages, NREM and REM sleep, which alternate within roughly 90-minute cycles throughout the night. REM sleep is characterized by low-amplitude, fast electroencephalographic (EEG) oscillations, muscle atonia, and rapid eye movements (Aserinsky & Kleitman, 1953). NREM sleep is further divided into 3 sub-stages, which correspond to increasingly deeper stages of sleep (Iber, Ancoli-Israel, & Quan, 2007). Stage 1—a transition state between wakefulness and sleep—consists of relatively low voltage (2-7 Hz) activity mixed with alpha activity (<50% of a 30 second period). Stage 2, which makes up approximately 50% of the night's sleep, is characterized by the appearance of sleep spindles and/or K complexes (see Figure 1) (Carskadon, Dement, & others, 2000). Stage 3 sleep—previously separated into stage 3 and 4—is referred to as slow wave sleep (SWS) and consists of a prevalence of low-frequency cortical EEG oscillations (Iber et al., 2007). These sleep stages are characterized by dramatic changes in brain electrophysiology (see Figure 1 for EEG correlates), neurochemistry, and functional anatomy making them biologically distinct from the waking brain and also from one another (Hobson & Pace-Schott, 2002). As a result of these distinct differences between sleep stages, sleep cannot be treated as one homogeneous physiological state that may or may not affect memory. Rather, each sleep stage may possess a set of physiological and neurochemical mechanisms that contribute uniquely to memory processing.

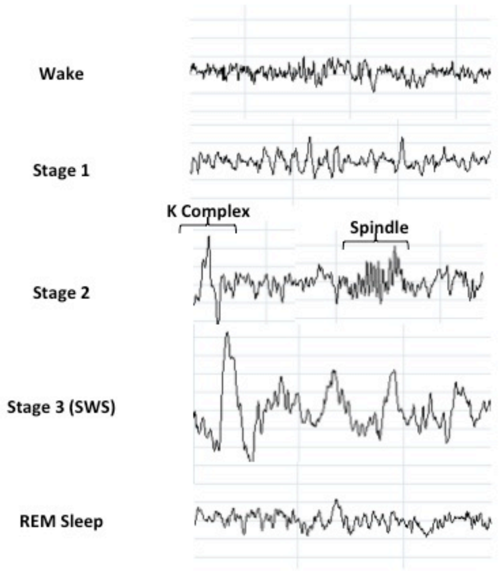

Figure 1: Stages of sleep and EEG correlates

Possible Functions Of Sleep

Humans spend approximately one third of their lives asleep and yet there is little scientific consensus for *why* we must sleep. From an evolutionary perspective it seems counterintuitive that sleep would have any benefit to an organism as reduced responsiveness to potentially threatening stimuli during sleep may decrease survival. And yet, it has been shown that nearly all animals sleep for some period of time (Siegel, 2005). Moreover, studies demonstrate that a lack of sleep causes severe cognitive and emotional problems in humans (Brown, 2012; Kerkhof & Van Dongen, 2010; Vandekerckhove & Cluydts, 2010). In addition, animals who are deprived of sleep for extended periods of time show temperature and weight dysregulation and ultimately die of infection and tissue lesions (Rechtschaffen & Bergmann, 1995). Such evidence, therefore, strongly argues in favor of sleep playing an important and necessary role in maintaining the overall fitness of an organism. Or, to put it more succinctly, as renowned sleep scientist Allan Rechtscaffen once remarked, “If sleep doesn’t serve an absolutely vital function, it is the biggest mistake evolution ever made” (Stickgold, 2006).

Exactly what that function might be, however, has been under some debate. Some researchers propose that sleep plays a role in conserving energy (Berger & Phillips, 1995), repairing cells (Oswald, 1980), thermoregulation (Rechtschaffen & Bergmann, 1995), and metabolic regulation (Knutson, Spiegel, Penev, & Van Cauter, 2007). But, although sleep may play a role in all of these processes, such functions could also be achieved during a period of quiet wakefulness and, thus, do not account for the loss of consciousness and responsiveness to threats that occur during sleep (for review, see Rasch & Born, 2013). These particular features of sleep— a natural and reversible state of reduced responsiveness to external stimuli and relative inactivity, accompanied by a loss in consciousness (Carskadon et al., 2000)—suggest that sleep may have evolved “for the brain” (Hobson, 2005). More specifically, it has been proposed that sleep may play an active role in functions including: detoxifying the brain from free radicals (Reimund, 1994) and cellular waste (Xie et al., 2013), maintaining synaptic homeostasis (Tononi & Cirelli, 2006), and forming and strengthening memory (Diekelmann & Born, 2010; Ellenbogen, Payne, & Stickgold, 2006; Stickgold, 2005; Wilson & McNaughton, 1994). The role of sleep in strengthening memory, in particular, has received considerable attention within the scientific community in the last ten years and is the focus of this review due to its implications for selective memory enhancements.

Historical Overview of Sleep And Memory Research

The beneficial relation between sleep and memory has a surprisingly long history, despite what appears to be only a recent resurgence in the scientific community. In first century AD, Roman philosopher Quintilian stated, “what could not be repeated at first is readily put together on the following day; and the very time which is generally though to cause forgetfulness is found to strengthen the memory.” (Quintilian 1856/2006). In the early nineteenth century British psychologist David Hartley proposed dreaming might alter the strength of associative memory links in the brain (Hartley, 1801). Nevertheless, it was not until the early twentieth century when the first systematic experiments investigating the effects of sleep on memory occurred.

In a classic experiment in 1924, testing Ebbinghaus’s theory of decay, Jenkins and Dallenbach demonstrated that memory retention was better after a period of sleep than after an equivalent period of wakefulness (Jenkins & Dallenbach, 1924). However, partially based on the common assumption at the time that sleep was a homogenous state in which the brain was “turned off” (Dement, 1998), Jenkins and Dallenbach concluded that the benefit of sleep was passive and thus a result of a lack of interference from new external stimuli while sleeping.

Moreover, the perspective that sleep is a homogenous state during which the brain is inactive, which has been referred to as the “passive process theory” (Dement, 1998), likely made the study of sleep and its function uninteresting to cognitive scientists. As a result, little progress occurred in the field prior to the 1950s (Dement, 1998). However, two important developments prior to the 1950s began to change the scientific community’s perception of the function sleep and helped usher in a renaissance of sleep research. The first development occurred in 1875 when Scottish physiologist Richard Canton demonstrated electrical activity in animals during sleep (Canton, 1875). This eventually paved the way to the development of polysomnography—including electroencephalography (EEG)—in the 1950s and the subsequent study of neural activity during sleep. The second development came from the field of psychoanalysis—one of the dominant psychological disciplines at the time—and, more specifically, Sigmund Freud's writings on dream interpretation (Dement, 1998). For the first time, psychologists began to recognize that the mind might be active during parts of sleep, specifically when an individual was dreaming (Freud, 1950), thus leading to an increasing desire to find a physiological marker of dreaming.

A major breakthrough that cast doubt on the hypothesis of a 'quiet' brain during sleep came in 1953 with Aserinsky and Kleitman's seminal paper chronicling the discovery of rapid eye movement (REM) (Aserinsky & Kleitman, 1953). This discovery demonstrated that sleep was neither "passive" nor homogenous, but instead was comprised of qualitatively different stages of activity that cycled throughout the night. In the years that followed, sleep researchers distinguished between REM sleep and Stages 1-4 of non-REM (NREM) sleep (Rechtschaffen & Kales, 1968). Moreover, sleep researchers also began to investigate the different roles that each of these stages might have on different aspects of cognition, such as memory. Initially, due to interest in establishing a function for dreaming, much of the focus was on REM sleep (Siegel, 2001; Tilley & Empson, 1978) although, due to initially weak evidence (Siegel, 2001), the focus eventually shifted to examining both REM and NREM sleep stages (Ellenbogen et al., 2006; Stickgold, 2005).

Influence Of Sleep On Stages of Memory

Memory processing is conventionally divided into three stages: encoding, consolidation, and retrieval. Although the effect of sleep on memory processing is necessarily measured at retrieval, the effect of sleep on memory processing is primarily thought to influence both the encoding and consolidation stages. It is clear that sleep before a learning episode is important for memory as sleep deprivation has been shown to disrupt encoding (for review, see Walker & Stickgold, 2006). Particular interest, however, has focused on the effects of post-learning sleep and memory consolidation (for review, see Diekelmann & Born, 2010; Ellenbogen, Payne, & Stickgold, 2006; Stickgold, 2005).

Memory consolidation is generally thought to involve two different types of processes: synaptic consolidation and systems consolidation (Dudai, 2012). Synaptic consolidation is initiated immediately and accomplished within hours to one day after learning (Dudai, 2004). It is considered universal in that is has been described in all species and memory tasks investigated to date, as long as the task results in long-term memory (i.e., lasting more than 24 hours with the exception of long-term potentiation, which is a considerably shorter process). Systems consolidation takes much longer, days to weeks, and is the process by which memories that are initially dependent upon the hippocampus undergo reorganization and may become more hippocampal-independent (Dudai, 2004).

It has been proposed that systems consolidation takes place preferentially during sleep (Diekelmann & Born, 2007). Specifically, newly encoded memories are *reactivated* during sleep to be redistributed to long-term storage sites in the neocortex. Moreover, because these processes occur offline, they may interfere with the brain's normal processing of external stimuli preventing interference from encoding processes (Diekelmann, Biggel, Rasch, & Born, 2012; Diekelmann & Born, 2007). Synaptic consolidation, on the other hand, may occur equally well during periods of both wakefulness and sleep (in particular REM sleep) (Born & Wilhelm, 2012; Diekelmann & Born, 2010).

Sleeps Role In Systems Consolidation

In order to conceptualize the function of sleep as a process that supports systems consolidation researchers typically use the *standard two-stage model of memory* as a basis (Diekelmann & Born, 2010; Marshall & Born, 2007). The standard two-stage model of memory assumes two separate memory stores: a memory store that learns quickly and only holds information temporarily and another that learns at a slow rate but also shows a slow rate of forgetting and stores information long-term. The fast-learning temporary and slow-learning long-term stores are represented by the hippocampus and neocortex, respectively (McClelland, McNaughton, & O'Reilly, 1995). New information is initially encoded in parallel into both the temporary and long-term stores. Then, during subsequent periods of consolidation, the newly encoded memory traces are repeatedly reactivated and gradually become reorganized such that the representations in the long-term store are strengthened. Over time, the repeated reactivation of new memories in the hippocampus in conjunction with older—and related—memories result in the integration of the newly encoded memories into pre-existing knowledge networks within the neocortex. Moreover, repeated reactivation of temporary memories in the hippocampus results in a gradual redistribution—over a period of days and years—to neocortical networks and, in the case of more generic and semantic memories, ultimately lose their dependence on the hippocampus (McClelland et al., 1995; Zola-Morgan & Squire, 1990). However, some theorize that very detailed episodic recollections may potentially be retained by hippocampus indefinitely, even after years of consolidation (Nadel, Winocur, Ryan, & Moscovitch, 2007).

Since both the temporary and long-term memory stores are also used for encoding new information, encoding would likely interfere with consolidation process. Therefore, in order to prevent such interference it has been hypothesized that reactivation and redistribution of memories during consolidation takes place during offline periods (i.e., during sleep when there is no encoding) (Born & Wilhelm, 2012; Diekelmann & Born, 2010). In addition, it has been suggested that the reactivation and redistribution of memories to the neocortex for long-term storage can also promote the extraction of relevant features of new memories, whereas irrelevant features may be erased (Born & Wilhelm, 2012). This extraction of relevant features has been demonstrated when participants were given a task with a hidden rule to learn. Participants who slept after the initial training session were significantly better at gaining insight into the rule, but only if they practiced the task before sleeping ensuring that they had encoded the task, which could later be re-processed during sleep (Wagner, Gais, Haider, Verleger, & Born, 2004). Thus, sleep may not merely preserve all memory, but rather sleep may selectively preserve relevant information (Born & Wilhelm, 2012). In the following sections I will first describe the general mechanisms by which sleep may consolidate memories and then discuss how sleep may be selective by what information it consolidates.

‘Reactivation' As The Mechanism By Which Sleep Consolidates Memory

One mechanism by which memories could be consolidated during sleep is through reactivation. Extracellular in vivo studies investigating SWS physiology have found that neocortical neurons will spontaneously reactivate during SWS, which could lead to strengthening of memory traces (Steriade & Timofeev, 2003). Along the same vein, several studies in animals have demonstrated that recently acquired hippocampus-dependent memories are ‘replayed’ (i.e., same patterns of neural firing in hippocampus observed during learning were repeated) during SWS implicating offline consolidation processes (O’Neill, Senior, & Csicsvari, 2006; Wilson & McNaughton, 1994). Studies of recently acquired memories for spatial navigation have found that replays occur in the hippocampus both during periods of wakefulness and sleep. During wakefulness, memories are replayed backward (Foster & Wilson, 2006) and during sleep memories would be replayed forward (for review, see (Suzuki, 2006) suggesting different processes. In particular, that initial learning relies on reverse replay whereas consolidation occurs during forward replay (Ellenbogen et al., 2006).

Similar evidence has been reported in humans using a virtual maze task and positron emission tomography (PET) scanning (Peigneux et al., 2004). Initial learning during waking hours was associated with hippocampal activity, which then re-emerged during SWS. More importantly, the amount of SWS reactivation in the hippocampus was proportional to the amount of task improvement the next day, suggesting that this reactivation is associated with offline memory enhancement. Building on the idea that SWS is actively involved in declarative memory consolidation, Rasch, et al. (2007) demonstrated that individual memories could be actively reprocessed during SWS sleep. Using a classic cue-dependent recall task, Rasch and colleagues paired a spatial memory task with the smell of a rose at learning. Then, rather than re-present the odor at retrieval, Rasch et al. re-presented the odor during subsequent SWS that night, presumably when consolidation was occurring. Compared to the control condition, where no odor was presented again during SWS, the reintroduction of the rose scent at night resulted in significant improvement in recall the next day. Most compelling, however, the re-presentation of the rose scent resulted in greater reactivation of the hippocampus during SWS.

Using a similar paradigm, Rudoy, et al. (2009) paired related sounds (e.g., cat meow) with object-location pairs (e.g., picture of a cat) during learning. While participants slept, some of the sounds were re-presented during SWS sleep. Subsequent memory performance the next day was better for the cued items than for the non-cued, thus demonstrating that sleep can benefit memory by selectively reactivating and consolidating recently learned information.

It has also been suggested that these reactivations are evidence of a transfer of memory representations to neocortical regions (Gais et al., 2007; Takashima et al., 2006), a hallmark of systems consolidation (Squire & Alvarez, 1995). In an fMRI study, Takashima et al (2006) tested recognition memory of neutral pictures at four different time points over a 3-month span. Across the 3 months, memory retrieval was progressively associated with less hippocampal activation and more ventral medial prefrontal cortex activation. In another fMRI study, Gais et al (2007) instructed participants to learn word pairs and then either allowed participants to sleep, or deprived them of one night of sleep. Participants then returned to the lab 48 hours later and recalled the word pairs in the fMRI scanner. Functional connectivity analyses revealed greater connectivity between the hippocampus and medial prefrontal cortex in the group that was allowed to sleep compared to the group that was deprived of sleep immediately after learning. Both groups were retested 6 months later and the group that slept after learning showed greater medial prefrontal cortex activation than those who were originally sleep deprived. The changes in connectivity across time suggest that initial sleep is critical for consolidating new memories into neocortical storage areas.

As it has been noted above, an abundance of evidence supporting reactivation as a mechanism by which memories are consolidated during sleep suggests this process occurs during periods of NREM sleep, and more specifically SWS. Indeed, various studies investigating the role different sleep stages play in memory consolidation suggest that SWS and specific physiological characteristics of SWS, is critical for declarative memory consolidation (Gais & Born, 2004b; Plihal & Born, 1997; Rauchs, Desgranges, Foret, & Eustache, 2005). Gais and Born (2004), reported superior recall among participants who slept during the first part of the night, which has a higher prevalence of SWS sleep than later in the night, compared to those who were awake for the same time period. More importantly, this effect was not seen in participants who slept during the second half of the night, during which relatively less SWS occurs. Additionally, Gais and Born (2004) found that experimentally elevating levels of acetylcholine appeared to diminish any benefit of sleep to declarative memory consolidation during SWS, suggesting that low levels of acetylcholine during SWS may play an important role in consolidating memories.

Sleep Is Selective About What Information Is Subsequently Consolidated

During waking hours, a vast amount of information is encoded by the brain and yet only a fraction of this information is eventually stored over the long term. This selective long-term storage of information is in fact advantageous, because indiscriminate storage of all information would likely lead to interference and impaired memory performance due to capacity overload. By this view, selectivity may represent an adaptive function of memory consolidation within the human memory system. Although the literature overwhelmingly suggests that not all memories benefit from sleep-dependent memory consolidation (Diekelmann, Born, & Wagner, 2010; Diekelmann & Born, 2010; Groch, Wilhelm, Diekelmann, & Born, 2013; Payne, Stickgold, Swanberg, & Kensinger, 2008; Payne et al., 2009; Oudiette, Antony, Creery, & Paller, 2013; Rauchs et al., 2011; Saletin, Goldstein, & Walker, 2011; Wagner, Gais, & Born, 2001; Wagner, Hallschmid, Rasch, & Born, 2006), the factors that determine what information will be selectively consolidated are not fully understood.

The currently dominant theory regarding sleep-dependent memory consolidation proposes that motivationally relevant, or salient, information (information that will be rewarded or important for the future) will be preferentially reactivated during sleep (Fischer & Born, 2009; Saletin et al., 2011; Wilhelm et al., 2011). Animal studies demonstrate that rewarded information is preferentially reactivated in the hippocampus and ventral striatum during sleep (Lansink et al., 2008; Lansink, Goltstein, Lankelma, McNaughton, & Pennartz, 2009). Along the same vein, Oudiette et al, (2013) demonstrated that rewarded information is preferentially reactivated during sleep in humans. Using the same paradigm described earlier in this review (Rudoy et al., 2009), Oudiette and colleagues (2013) instructed participants to remember the location of everyday objects presented on a screen. In order to manipulate reward each object was assigned a value that represented a future payoff (either low or high value) for successful subsequent memory retrieval. Sounds cues, which were paired with the high and low value items, were re-presented during SWS and periods of wakefulness. Interestingly, only low-value items were selectively enhanced by sleep, whereas memory for high-value items did not differ by consolidation type (i.e., wake or sleep). This perhaps suggests that there may also be some sort of contextual cue that plays a role in what information sleep selectively enhances.

Sleep can also selectively enhance information in the absence of an external reward. Wilhelm et al. (2011) demonstrated that the mere expectancy that a memory would be used in a future test determined whether sleep would significantly benefit subsequent memory performance. All participants learned word pair associates before a period of sleep or a comparable duration of wakefulness. Only participants who were informed about the retrieval test prior to sleep showed an enhancement in memory performance after sleep. The memory enhancement in the group expecting a memory test was also strongly correlated with features of SWS, such as slow oscillation activity and sleep spindle count.

Along the same vein, Rauchs et al (2011) and Saletin et al, (2011), both demonstrated using a directed forgetting memory paradigm, that sleep can selectively consolidate information that participants were cued to remember. Moreover, Saletin et al (2011), found that this selective enhancement was correlated with fast sleep spindle activity (a property of Stage 2 sleep, though also present in SWS) (Mölle, Marshall, Gais, & Born, 2002). Spindles (see Figure 1 for an example) are temporally connected to hippocampal ripples (Marshall & Born, 2007), which are high frequency field oscillations during which neurons replay previous waking activity (Buzsaki, Horvath, Urioste, Hetke, & Wise, 1992; Buzsaki, 1998), suggesting that sleep spindles in humans may reflect the same underlying process identified by replay in animals. Thus, reactivation during NREM sleep may selectively target memories that are salient or important to remember.

Alternate explanation for selectivity in memory after sleep

Although reactivation is the predominant theory for how memories are selectively consolidated, a recent alternate theory has emerged. The *synaptic downscaling theory* postulates that sleep is involved in regulating synaptic connectivity in the brain, principally in the neocortex (Tononi & Cirelli, 2003, 2006). SWS—and more specifically the magnitude of slow wave activity (SWA) of SWS—promotes the decrease of synaptic connections, resulting in a reduction in total synaptic weight. In terms of how this affects memory, the synaptic downscaling theory assumes that encoding of new information during wakefulness is associated with widespread upscaling of synaptic strength. Moreover, stronger memory traces result in stronger synaptic connections, whereas weaker memory traces result in weaker synaptic connections. Sleep, on the other hand, is associated with global downscaling of synaptic strength, which is necessary to counter waking activity synaptic potentiation and associated growth, which would otherwise exhaust available resources and space. Factors of SWS, specifically slow waves, convey LTP-mediated synaptic upscaling, while simultaneously representing a mechanism for downscaling (Born & Feld, 2012). This simultaneous strengthening of strong synaptic connections between neurons and eliminating weak synaptic connections between neurons promotes synaptic competition and it is possible that selectivity in memory after sleep may be an indirect consequence of this synaptic competition (Oudiette & Paller, 2013). Although an intriguing possibility, the synaptic homeostasis theory cannot account for some of the qualitative changes in memory observed after sleep, such as increased insight into hidden rules (Wagner et al., 2004), generalization, and abstraction (Gómez, Bootzin, & Nadel, 2006; Lau, Alger, & Fishbein, 2011). However in the current research we can explore whether memory enhancements after sleep are due to overall strengthening of strong memory traces (which would support both views) or due to other qualitative changes in how subsequent memory is represented (which would only support the active system consolidation hypothesis).

Selective Consolidation Of Emotional Information During Sleep

A common feature in the previous studies investigating selective memory consolidation after sleep is that saliency was externally motivated by the experimenter, either through assigning a reward value (Fischer & Born, 2009; Oudiette et al., 2013) or by designating relevance to future tasks (Saletin et al., 2011; Wilhelm et al., 2011). Although this line of research has important implications for different disciplines, such as education (by studying how new material can be emphasized for learning), it is also important to understand how reactivation might occur spontaneously during sleep-dependent consolidation, which would illustrate how memory is naturally consolidated during sleep. One way that this has been investigated is using emotional stimuli, which is often considered intrinsically salient to individuals.

There is increasing evidence that supports the theory that sleep selectively consolidates emotional memory (Atienza & Cantero, 2008; Bennion, Mickley Steinmetz, Kensinger, & Payne, 2013; Cairney, Durrant, Power, & Lewis, 2014; Hu, Stylos-Allan, & Walker, 2006; Jessica D. Payne et al., 2008; Lewis, Cairney, Manning, & Critchley, 2011; Payne & Kensinger, 2010, 2011a; Sterpenich et al., 2009; Wagner et al., 2006, 2001). Using a Remember/Know recognition memory paradigm, where participants had to judge whether they remembered (defined as the conscious *recollection* of vivid contextual details, such as "when" information was learned) or knew (defined as a feeling of *familiarity* for a stimulus, a feeling of having seen it before but not knowing why) a stimulus (Mickley & Kensinger, 2008), Hu et al., (2006) measured the effect of sleep on consolidation of emotional pictures. They compared consolidation of emotionally negative arousing and non-arousing neutral picture stimuli following a 12-hour period across the day (i.e., during wakefulness) or across an equivalent period at night containing sleep and found a specific emotional benefit only following sleep and not during wakefulness. However, the benefit was only observed for "Know" judgments. No benefit was seen for "Remember" judgments, which reflect more conscious recognition memory processes and, as a result, it unclear if sleep benefits explicit emotional memory.

Taking a different approach, Payne et al., (2008) examined how different components of negatively arousing memories change over periods of sleep versus wakefulness. In particular, they were interested in investigating if emotional scenes are stored as intact units, which are uniformly enhanced, or if different components of a scene undergo differential processing during sleep where there is a selective emphasis on what is considered most 'salient'. As stated earlier, central and emotional information is often remembered at the expense of background details (e.g., the weapon focus effect). Measuring the effect of a full night of sleep post learning, Payne et al, (2008) presented emotional (negative) and neutral objects on neutral backgrounds and then tested memory for the objects and backgrounds separately. They found a memory trade-off, where negative emotional objects were better remembered whereas memory for the neutral background associated with the negative object decreased. They hypothesized that individual components of a scene become unbound during sleep, allowing sleep to selectively preserve what is most salient (e.g., emotional information). These findings have been replicated in subsequent studies (Bennion et al., 2013; Payne & Kensinger, 2010, 2011a). Moreover, changes in emotional reactivity after sleep (Baran, Pace-Schott, Ericson, & Spencer, 2012; Walker & van Der Helm, 2009) suggests that sleep could more generally interact with emotional processing.

It is important to note that all of the previously mentioned studies have focused on the effects of post-learning sleep on memory for negative arousing events (Hu et al., 2006; Payne et al., 2008). Evidence investigating whether sleep has a role in consolidating positive emotional memories after learning is scant. Atienza and Cantero (2008) measured recognition memory performance for emotional and non-emotional images after a night of post-learning sleep or sleep deprivation. Their results indicated that sleep deprivation resulted in impairments in memory performance for positive and neutral images. However sleep deprivation did not significantly reduce recognition accuracy of negative images indicating that emotion and sleep may differentially influence recognition performance. However, as of yet, the effect of normal sleep on memory for positive stimuli remains relatively uninvestigated.

The effects of sleep may differ for negative vs. positive emotional memories particularly in light of evidence that positive and negative memories may differ in several important respects (Kensinger, 2004, 2009; Ochsner, 2000) as discussed in the previous section. Additionally it is unknown whether non-affective factors of emotion, namely distinctiveness, will also selectively influence consolidation during sleep. As a result, the influence of sleep on consolidation of positive and distinctive stimuli will be focus of the two experiments in this thesis.

Mechanisms For Consolidation Of Emotional Information During Sleep

Although NREM sleep is implicated in declarative memory consolidation for neutral information relevant to an organism, rapid eye movement (REM) sleep may be particularly influential for emotional processing during sleep (Ackermann & Rasch, 2014; Groch et al., 2013; M. Nishida, Pearsall, Buckner, & Walker, 2009; van der Helm et al., 2011; Wagner et al., 2001). In humans, the amygdala and hippocampus are more active during REM sleep than during wakefulness and several studies have demonstrated that REM sleep influences memory performance for negative emotional information (for review, see Walker & van der Helm, 2009). Moreover, REM sleep is associated with marked increases in cortisol, one of the stress hormones important for the modulation of emotional memory via interactions between the amygdala and hippocampus (Payne & Nadel, 2004). In a recent overnight study using the emotional memory trade-off paradigm, Bennion et al. (2013) demonstrated that elevated cortisol at encoding resulted in a selectively enhancement in memory for objects if participants slept directly after encoding.

Investigating the specific effects of REM sleep Wagner et al. (2001) have demonstrated that sleep preferentially enhances retention of previously learned emotional texts relative to neutral texts and that this affective memory benefit is only present following late-night sleep, which is rich in REM sleep. Using a nap paradigm, it has been recently shown that REM sleep neurophysiology may underlie the consolidation of emotional material (Nishida et al., 2009). Participants who napped for 90 minutes after the initial training session showed a significant and selective enhancement of emotional memory over participants who were awake for an equivalent period. Additionally, the extent of the enhancement was correlated with the amount of REM sleep and the speed of entry into REM (i.e., REM latency).

More recently, it has been suggested that REM sleep might protect the emotional salience of the information encoded, but not preferentially benefit emotional memory (Baran et al., 2012; Lewis et al., 2011). Baran et al. (2012) used an incidental memory task to investigate the benefit of sleep for emotional memory consolidation and found that sleep enhanced both negative and neutral memories. Additionally, they found that whereas REM sleep preserved the emotional reactivity of the negative memories (as assessed by valence and arousal ratings), there was no correlation for REM sleep and memory performance. A recent nap study by Payne and Kensinger, (2011a) also failed to find a REM-specific benefit to memory performance. They demonstrated that sleep preferentially preserved emotional (negative) aspects of complex experiences at the expense of neutral aspects, but that the enhancement in memory for the emotional aspects was correlated with time spent in SWS. Moreover, this preferential enhancement was further intensified across longer (24 hour and 3 month) delays, but only when a nap directly followed encoding, thus implicating SWS in consolidation of negatively salient information.

Complementary roles of REM and NREM sleep stages in selective consolidation of emotional information

The conflicting findings presented above suggest that conditions underlying preferential consolidation of emotional memories over sleep require further examination.

Most of the previous studies measured consolidation over the course of a full night's sleep, which includes both periods of NREM and REM sleep. Although all of these studies implicated REM sleep as being critical for strengthening emotional memories, they could not unequivocally exclude the influence of NREM sleep. Evidence reviewed in the previous section suggest that NREM sleep enhances memory for salient information (classified as salient due to its future relevance to the participant) that individuals are instructed to attend to and learn. In addition, the recent study by Payne and Kensinger, (2011a) suggested that NREM sleep, and specifically SWS, may influence emotional memory processing during sleep. It is possible that the initial strengthening of newly learned salient information or, more specifically, whatever was strongly encoded during initial learning, could occur during SWS sleep. Conversely, REM sleep could selectively preserve emotional reactivity, leading to an additional boost for those emotionally charged memory traces. A recent fMRI study investigating the roles of SWS and REM sleep over the course of an entire night on memory consolidation for emotional images demonstrated complementary roles of SWS and REM on consolidation processes (Cairney et al., 2014). This study demonstrated that emotionally charged memories might first be selectively reorganized from the hippocampus to the neocortex during SWS and then targeted for processing during subsequent REM sleep. Alternatively, NREM sleep could offer little benefit to subsequently recalled emotional information, as has been previously demonstrated (Wagner et al., 2001). It is clear that the roles of SWS and REM sleep in consolidation of emotional and otherwise salient information require further investigation.

The Current Study

The primary aim of the current research was to extend the existing literature examining how emotion influences what information is better remembered. This was accomplished by manipulating different stimulus attributes, both emotional and not emotional, that influence memory processing, and in particular, memory consolidation processes. Memory consolidation was examined by manipulating sleep, both in an overnight behavioral paradigm (Study 1) and a nap paradigm (Study 2), as previous research suggests that sleep provides the ideal conditions for memory consolidation to occur (Ellenbogen et al., 2006). Both studies used a memory trade-off paradigm, which was adapted from Kensinger et al. (2007). At encoding, participants viewed scenes consisting of a central item (which was either negative, positive, neutral, or visually distinctive but emotionally neutral) against a neutral background. After an interval, which included a period of sleep, participants received an incidental recognition test on the items and backgrounds presented separately. The advantage of this paradigm, compared to testing memory for intact pictures, is that memory for different components can be measured separately to investigate what information may be selectively enhanced. Previous work has demonstrated that emotion (Kensinger et al., 2007; Waring & Kensinger, 2009) and distinctiveness can elicit memory trade-offs (Campanella & Hamann, in preparationa, in preparationb). Theories suggest that emotion may influence memory trade-offs through memory consolidation (Payne et al., 2008; Payne & Kensinger, 2011b). However, in many of the previous studies, the effect of emotion on memory trade-offs only examined the influence of affective factors (i.e., emotional arousal and to a lesser extent valence). How non-affective characteristics, namely distinctiveness, elicit memory trade-offs is unknown and, as a result, was the focus of this dissertation. In Study 1, consolidation was investigated over the course of a full night of sleep, in order to replicate previous findings, which compared negative scenes to neutral and observed enhanced memory trade-offs for negative scenes after sleep (Payne et al., 2008), and extend those findings to investigate whether similar enhancements would also be observed for positive and distinctive scenes. Including both positive and distinctive scenes provided the opportunity to investigate whether valence, arousal, and distinctiveness were consolidated during sleep through the same mechanism or an overlapping one. In Study 2, the role of sleep in consolidating these scenes was further investigated by examining the relation between different components of sleep and memory performance using a nap paradigm during which polysomnography was collected. Of particular interest was whether the same stage of sleep mediated selective consolidation of emotional and distinctive scenes, which would suggest that these factors might be consolidated through a common mechanism.

Investigating how memory trade-offs develop and change during consolidation (primarily during sleep) provides a direct way of examining the question of how sleep-dependent consolidation processes may preferentially select some information about an experience for long-term storage, while allowing other information in memory to deteriorate. To be more specific, a memory-trade paradigm allows us to separate central components from the peripheral background at retrieval and test memory for each component separately. In the current literature, it is still unclear how information is selectively preserved during sleep. The findings reviewed above suggest that sleep-dependent consolidation is essential for the preservation of emotional information over time and could additionally play a critical role in selectively preserving emotional aspects of complex experiences. However the question of what emotional aspects are selectively preserved remains unanswered.

In addition to the theoretical contributions, the outcomes of this research are important to human health and disease because findings from the current studies may offer important insights into affective clinical disorders, such as major depression and PTSD. In these affective disorders, the same memory biases described earlier exist in an exaggerated form. Specifically, both disorders are associated the tendency to remember negative information at the expense of other information (for review, see Payne & Kensinger, 2010). Such disorders are also associated with marked changes in REM sleep physiology, including excessive REM sleep and shortened REM sleep latency (Cartwright, 1983). In addition, cortisol changes observed in depression and PTSD could interact with changes in REM sleep and emotional memory processing during sleep (Payne, Nadel, Britton, & Jacobs, 2004). Therefore, understanding how sleep is involved in emotional memory consolidation, and more specifically consolidation of emotional memory trade-offs is critical for understanding healthy emotional processing as well as its dysfunction.

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The Effect of a Full Night of Sleep on Memory Consolidation of Emotional and Distinctive Composite Scenes

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Abstract

Emotion has selective effects on episodic memory. For example, episodic memory for salient aspects of emotional scenes is often enhanced whereas memory for background, neutral information is impaired, a phenomenon referred to as the emotional memory trade-off effect. This selectively in memory typically increases after a delay including sleep; suggesting sleep may selectively enhance emotional memory via consolidation. Previously, it has been demonstrated that distinctive, non-emotional stimuli can elicit similar memory trade-offs, suggesting that similar cognitive processes may underlie trade-offs for salient emotional and neutral information. However, it is unknown whether sleep also selectively enhances memory for distinctive, non-emotional information. The aim of the current study was to investigate the effect of sleep on memory trade-offs for distinctive and emotional information. At encoding, subjects viewed scenes consisting of a central item (either negative, positive, neutral, of visually distinctive but emotionally neutral) against neutral scene backgrounds. After a 12-hour interval, which either included a full night of sleep or an equivalent period of daytime wakefulness, recognition memory was tested for the objects and neutral backgrounds. Sleep data was collected using Zeo wireless devices. There was no behavioral difference in memory performance between sleep and wake groups. There was, however, a non-significant correlation between sleep duration and memory for backgrounds paired with distinctive scenes suggesting sleep may play a role in consolidating neutral, and thereby less salient, information and demonstrates a need to further elucidate the mechanisms by which sleep selectively consolidates information.

Keywords: Emotional memory, distinctiveness, sleep-dependent consolidation, memory trade-off

The effect of a full night of sleep on memory consolidation of emotional and distinctive composite scenes

The capacity to remember past events is fundamental and yet we only remember a fraction of past experiences. Remembering absolutely everything would likely result in a system overload and leave few resources to engage in other cognitive functions, which explains we only remember selective pieces of information. Although a multitude of factors can affect the likelihood that an event will be remembered, one particular factor which is thought to enhance memory is emotion (McGaugh, 2004). Increasing evidence suggests that emotion may enhance memory through sleep-dependent consolidation processes (Payne et al., 2008; Payne & Kensinger, 2011a; Wagner et al., 2001). Emotion is typically defined by its affective dimensions, namely emotional arousal (how strong the emotion is) and valence (how unpleasant or pleasant a stimulus is). However emotion can also be defined by non-affective characteristics, such as distinctiveness (how atypical something is). Research measuring the enhancing effects of emotion on memory typically measure the effects of the affective characteristics of emotion, and more specifically the role that emotional arousal has in enhancing memory after sleep. As a result, it is currently unclear how factors such as distinctiveness may enhance memory through sleep-dependent consolidation. The goal of the present research was to address these issues, by extending previous research to also investigate how valence and distinctiveness may modulate memory consolidation during sleep.

Over the past decade there has been increasing evidence to suggest that sleep plays a beneficial role in memory consolidation processes (Ellenbogen et al., 2006; Maquet, 2001; Stickgold, 2005). More specifically, performance on a variety of different memory tasks is better after a period of sleep than after an equivalent period of wakefulness (Diekelmann & Born, 2010; Stickgold, 2005; Walker & Stickgold, 2006). Moreover, it has been demonstrated that sleep's role in memory consolidation is active and that subsequent behavioral benefits on memory are not merely a result of passive protection from interfering stimuli during sleep. To be specific, in addition to improving subsequent memory performance, sleep has also been shown to protect episodic memories from subsequent interference (Alger, Lau, & Fishbein, 2012; Ellenbogen, Hulbert, Stickgold, Dinges, & Thompson-Schill, 2006). In addition, studies demonstrate that there are relations between improvements in subsequent episodic memory performance and physiological properties of sleep (Alger et al., 2012; Gais & Born, 2004b; Marshall, Helgadóttir, Mölle, & Born, 2006), and that sleep even promotes reactivation of recent memories (Peigneux et al., 2004; Wilson & McNaughton, 1994). In summary, a growing body of evidence suggests that sleep actively contributes to consolidation of memory.

An emerging theory related to sleep-dependent memory consolidation suggests that sleep is selective in what type of information it consolidates and that information that is deemed most 'salient' (i.e., important or relevant to remember) is preferentially consolidated after a period of post-learning sleep (Stickgold & Walker, 2013; Wilhelm et al., 2011). Emotional information is thought to be naturally salient (for discussion, see Waring & Kensinger, 2009) as it helps individuals avoid aversive situations and seek out rewarding situations, thus increasing survival. Studies, not directly measuring sleep, support this view as emotional information is often better remembered than neutral (Hamann, 2001; LaBar & Cabeza, 2006; McGaugh, 2004). The enhancing effects of emotion on memory are often magnified after a longer delay (≥ 24 hours) (Sharot & Yonelinas, 2008), suggesting that emotion influences offline memory consolidation processes, which may include a period of sleep. Studies investigating the effect of sleep on memory consolidation for emotional information support this idea for both a full night of sleep (Hu et al., 2006; Wagner et al., 2001) and a 90 minute nap (Nishida et al., 2009). Moreover, the benefits of sleep on emotional memory can be long-lasting (up to four years) if a period of sleep occurred directly after the initial learning period (Wagner et al., 2006).

It has been shown that emotional memories are not remembered in veridical form. That is, all aspects of an emotional experience are not equally remembered. Instead, emotion effects on memory are selective: memory for salient elements is enhanced at the expense of peripheral details or background (Buchanan & Adolphs, 2002; Reisberg & Heuer, 2004). A well-known example of this phenomenon is the *weapon focus effect*, during which victims of a crime will often preferentially remember the weapon (i.e., the salient detail) at the expense of background details, including the face of the perpetrator (Loftus, Loftus, & Messo, 1987). More generally, this phenomenon is referred to as an *emotion-induced memory trade-off* (Kensinger et al., 2007). Memory trade-offs have been typically examined by measuring memory for emotionally arousing items embedded within emotionally neutral scenes. When a negatively arousing item (e.g., a snake) is placed in front a neutral background (e.g., a desert) individuals will preferentially remember the arousing central item, compared to the neutral item (e.g., a pair of boots) placed in front of the same neutral background (Kensinger et al., 2007; Waring & Kensinger, 2011). As a result, a trade-off is created in which the emotional memory advantage is only seen for the arousing item, whereas memory the background behind that arousing item is diminished. Therefore, these observed memory trade-offs demonstrate that emotion has a selective influence on information that is later remembered, with emotion acting as a filter for emotional central aspects of a scene—higher priority information—that is then enhanced with respect to subsequent memory. Furthermore, it has been demonstrated that sleep interacts with emotion to magnify these observed memory trade-offs (Payne et al., 2008; Payne & Kensinger, 2010).

A leading explanation for how memory trade-offs may be selectively enhanced during sleep is that emotionally salient elements of a stimulus, specifically the most arousing elements, are filtered by attracting greater attention and processing resources at encoding, resulting in enhanced memory encoding for those salient elements and, subsequently, enhancing memory consolidation (Bennion, Ford, Murray, & Kensinger, 2013; Payne & Kensinger, 2010). Preferential recruitment of attention and processing resources by emotionally arousing and salient elements also decrease the availability of these resources for encoding and consolidation of other stimulus elements, such as the background, leading to impaired memory for those background elements (Easterbrook, 1959; Kensinger et al., 2007). Various eye-tracking studies, which measure overt attention, have established that emotional arousal attracts attentional and cognitive processing resources (Christianson et al., 1991; Mickley Steinmetz, Waring, & Kensinger, 2013; Riggs et al., 2011).

The current proposed mechanism for memory trade-offs (Easterbrook, 1959; Kensinger et al., 2007), however, does not account for other emotional factors that might also influence memory trade-offs. One factor that may affect allocation of attention and subsequent memory performance is valence (how pleasant or unpleasant a stimulus is). Studies suggest that negatively and positively valenced information may differentially attract attentional and cognitive resources, and specifically that negative stimuli may preferentially attract attention relative to positive and neutral stimuli (Christianson & Fällman, 1990; Eastwood, Smilek, & Merikle, 2001; Smith, Cacioppo, Larsen, & Chartrand, 2003; Talmi et al., 2007), and cause individuals to elaborate more regarding negative information thus attracting more cognitive resources (Kensinger & Corkin, 2004; Talmi & Moscovitch, 2004). Therefore, it is possible that increased attention at encoding and increased elaboration after encoding would increase the likelihood that negative emotional information is preferentially consolidated and more vividly remembered relative to positive and neutral information. Waring and Kensinger (2009) examined the effect of valence on memory trade-offs after a short (10 minute) and long (24 hour) delay and found that young adults showed a memory trade-off for negative scenes after a long delay, suggesting that emotional valence differentially influences encoding and subsequent consolidation processes. However, more recent unpublished data in our laboratory demonstrated that both negative and positive emotion elicited memory trade-offs of the same magnitude after a 24-hour delay, suggesting that emotional valence may also determine what information is preferentially encoded and consolidated (Campanella & Hamann, in preparationa). It is important to note, however, that neither study directly measured the effect of valence on consolidation. As a result, it is unclear whether sleep differentially consolidates valenced information or if emotional arousal acts as the primary filter for what information is selectively consolidated during sleep.

Another factor that impacts allocation of attention and subsequent memory performance is distinctiveness. Prior work has demonstrated that, like emotional arousal, distinctiveness can also attract attentional and cognitive processing resources (Blackford et al., 2010; Itti & Baldi, 2009; Mitchell et al., 1998; Pickel, 1998; Ranganath & Rainer, 2003). Similar influences by emotion and distinctiveness on attentional and cognitive processing might be explained by common features of distinctive and emotional stimuli, including being more unexpected, perceptually unusual, or out of context in a given environment (Ochsner, 2000). In addition, the amygdala, which may influence memory by mediating attention at encoding shows increased responsiveness to both emotional stimuli (Hamann et al., 1999) and perceptually unusual stimuli (Blackford et al., 2010). In the context of memory trade-offs, some argue that unusualness (which shares perceptual features with distinctiveness) could also account for selective memory for elements in a scene (Mitchell et al., 1998; Pickel, 1998), whereas other findings suggest that selective memory for emotional scenes is solely a result of emotional arousal (Christianson et al., 1991). Recently, in an unpublished experiment using the memory trade-off paradigm, we compared the separate effects of emotion and visual distinctiveness on memory trade-offs and found that both emotion and distinctiveness elicited memory trade-offs of the same magnitude (Campanella & Hamann, in preparationa). Moreover, the memory trade-off remained for the distinctive scenes when emotional arousal was equated between the distinctive and neutral scenes, suggesting that distinctiveness on its own is enough to filter information for selective memory processing (Campanella & Hamann, in preparationb).

In summary, recent evidence suggests that emotional arousal, valence, and distinctive may filter salient information for subsequent memory processing through a common mechanism. Studies suggest that sleep selectively consolidates information that is highly salient (Wilhelm et al., 2011), an example being emotional information (Hu et al., 2006; Payne & Kensinger, 2010; Wagner et al., 2001), or even distinctive information. However, the exact mechanism by which emotional information is filtered for sleep-dependent consolidation is unknown. Emotional arousal is currently thought to be the primary determinant for what information is preferentially consolidated during sleep (Payne & Kensinger, 2010). However, this view ignores the influence that factors such as distinctiveness, which also elicit memory trade-offs (Campanella & Hamann, in preparationa, in preparationb), may have on selecting information for preferential consolidation during sleep.

The goal of the current study was to investigate the effect of a full night of sleep on consolidation of negatively arousing, positively arousing, neutral, and distinctive (but emotionally neutral) scenes. Participants were presented with pictures of scenes consisting of a target item (either negative, positive, neutral, or distinctive but emotional neutral) superimposed over neutral indoor and outdoor background scenes. After a 12 hour delay, during which participants went home and slept or experienced an equivalent period of daytime wakefulness, participants returned to the lab for an unannounced recognition test where they were tested on the central items and backgrounds separately in order to assess memory for each of these two elements. Because evidence suggests that emotion (Christianson et al., 1991; Hamann et al., 1999; Riggs et al., 2011) and distinctiveness (Blackford et al., 2010; Itti & Baldi, 2009; Mitchell et al., 1998; Pickel, 1998; Ranganath & Rainer, 2003) both preferentially attract attentional and cognitive processing resources, it was predicted that this preferentially allocation of resources would serve to filter emotional and distinctive central items for preferential consolidation during sleep. Preferential consolidation of these central elements would thus result in an enhanced memory trade-offs for individuals who slept during the intervening period between encoding and the recognition test, compared to individuals who spent the intervening period awake. Alternatively, because some evidence suggests that negatively valenced information attracts more attentional (Smith et al., 2003; Talmi et al., 2007) and cognitive resources (Talmi & Moscovitch, 2004) than positively valenced information, it is possible that only negative and distinctive scenes would be preferentially consolidated resulting in enhanced memory trade-offs for negative and distinctive scenes after sleep. Moreover, demonstrating that sleep preferentially consolidates central elements of distinctive scenes, as has been previously demonstrated with emotional scenes (Payne et al., 2008; Payne & Kensinger, 2011a), would suggest that the previously reported selectivity in sleep-dependent emotional consolidation could also result from distinctiveness and other non-affective factors that also capture attention to tag information as 'salient'. This suggests a broadening of current theoretical views for how sleep mediates the memory trade-off effect to include the role of non-affective factors.

Methods

Participants

Sixty-two students from Emory University participated for payment or class credit. Twenty-four participants were excluded from the final analysis for various reasons: eleven participants were excluded for suspecting a memory test[1], eleven participants were excluded for poor memory data[2], and two participants were excluded for not providing sleep data. The final data set included thirty-eight students from Emory University (mean age= 19.37 years, *SEM*= 0.17). Participants self-selected into one of two conditions: either a sleep-12 hour-interval condition (N= 19, 14 females) or a wake-12 hour-interval condition (N= 19, 16 females). Participants in the sleep-interval condition viewed the stimuli sometime between 8-9 pm and were tested 12 hours later, at 8-9 am the following morning, after a full night of sleep. Participants in the wake-interval group viewed the stimuli at 8-9 am in the morning and were tested 12 hours later, at 8-9 pm. In addition, participants in the wake-interval condition were told not to nap during the 12-hour interval (Figure 1, for a diagram of experimental conditions).

All participants were native English speakers with normal to corrected-to-normal vision. No participant reported a history of sleep disorders or was taking medications that might affect their sleep cycle. As in similar studies of sleep and memory, participants with abnormal sleep patterns, defined as habitual sleep onset after 2 am, averaging less than 6 hours sleep duration per week were excluded from participating. Participants were also instructed not to consume alcohol or caffeine for the duration of the study. Furthermore, participants were asked to keep a sleep log during the week prior to the first session. On average participants slept an average of 7.99 hours per night (*SEM*= 0.14). There were no systematic differences in average sleep per night for the sleep and wake groups (*M*= 8.12, *SEM* =0.22 vs. *M*= 7.86, *SEM*= 0.16, *p*= 0.35). In

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[1] Seven of these participants were in the sleep-delay group and four participant were in the wake-delay group

[2] Corrected recognition performance for neutral backgrounds was less than zero

addition, Epworth Sleepiness Scales were collected to measure daytime sleepiness and no significant systematic differences were observed between sleep and wake groups (*M*=9.05, *SEM*=0.81 vs. *M*= 7.05, *SEM*=0.79, *p*= 0.09). Complete demographics information on all participants is included in Table 1. Written informed consent was obtained from all participants and the study was approved by the Emory University Institutional Review Board.

Materials

Composite scenes

Visual composite scenes were used in this study the effect of sleep on memory trade-offs. The visual stimulus set used to test the effect of sleep on memory trade-offs was composed of 240 items (60 negative, 60 positive, 60 visually distinctive but emotionally neutral, and 60 neutral items) and 240 neutral backgrounds. Negative, positive, and neutral items were taken from those used in prior studies (Kensinger, Garoff-Eaton, & Schacter, 2007a; Waring & Kensinger, 2009). In order to create distinctive but emotionally neutral items, neutral items (e.g., a television) were modified through Photoshop (e.g., color overlay and pattern fill). Additional distinctive items, primarily chimeric animals and digitally manipulated items (e.g., a briefcase made of straw), which were rated by an additional group of participants as emotionally neutral were obtained from various internet photo-sharing sites.

Subjective emotional arousal and distinctiveness ratings for all the items were collected from all participants using a 1-5 Likert scale (1= low arousal to 5= high arousal). Emotional arousal ratings differed significantly between emotional and distinctive item categories, distinctive and neutral item categories, and emotional and neutral item categories (see Table 2 for breakdown of arousal ratings). Subjective distinctiveness ratings for all items were also collected from all participants using a 1-5 Likert scale (1= not visually distinctive, typical to 5 = very visually distinctive, atypical). Distinctiveness ratings differed significantly between emotional, distinctive and neutral item categories (see Table 2 for breakdown of distinctiveness ratings).

Backgrounds consisted of neutral indoor and outdoor scenes from the International Affective Picture System (IAPS; Lang, Bradley, & Cuthbert, 2008) along with some additional neutral images taken from public domain photo-sharing internet sites. All backgrounds were formatted to a size of 1000 x 750 pixels.

Composite scenes were created by pairing items from each stimulus category with neutral backgrounds. To be more specific, negative (e.g., a spiked weapon), positive (e.g., treasure chest), distinctive but emotionally non-arousing (e.g., chimeric animal that was part kangaroo, part lemur), and neutral items (e.g., a pair of boots) were individually paired with neutral backgrounds (e.g., a desert scene). Composite scenes were matched for item size, item location, visual complexity, and the semantic congruency of item and background scene.

The stimulus category of items combined with each background was counterbalanced across participants (see Figure 2 for example) to control for systematic stimulus effects of items and backgrounds. The resulting encoding lists contained of 160 composite scenes consisting of an item (40 negative, 40 positive, 40 distinctive, and 40 neutral) against a neutral background. The order of presentation for composite scenes at encoding was also counterbalanced across participants to control for order and carryover effects. Each encoding list was therefore further broken down into four lists: each containing 10 composite scenes from each category (i.e., 10 negative composite scenes, 10 positive composite scenes, 10 distinctive composite scenes, and 10 neutral composite scenes).

Verbal paired associates

In order to establish that any differences in memory performance were not due to the time of day in which participants were tested, two lists of semantically related verbal paired associates were compiled from lists used in other studies (Gais & Born, 2004a; Payne et al., 2012). All the verbal paired associates were previously equated by Gais and Born (2004) for concreteness, emotionality, imagery, meaningfulness, potency, and valence (see Appendix 1 for both lists). Each list consisted of 40 verbal paired associates. Participants were randomly assigned to one of the two lists.

Questionnaires for alertness, sleepiness, and mood

Three questionnaires were administered to assess subjective alertness (Stanford Sleepiness Scale; Hoddes, Zarcone, & Dement, 1972), daytime sleepiness (Epworth Sleepiness Scale; Johns, 1991) and mood at the time of testing (PANAS, Watson, Clark, & Tellegen, 1988) (see Appendix 2 for more detailed description). In order to assess whether mood differed based on when participants were tested, only the scale "I feel this way now" was used for the final analysis.

Sleep measurements

A wireless home sleep-stage monitoring device (Zeo, Inc.) was used to measure sleep architecture. The Zeo system includes a clock base station and an adjustable headband that is worn on the forehead, recording approximately at the Fp1-Fp2 locations. The headband includes sensors that collect electrophysiological data from a single channel, preprocess the data (by amplifying the signal and filtering noise), and transmit the data wirelessly to the clock base station. A microprocessor in the clock base station uses the preprocessed signal to calculate sleep stages in accordance with standard Rechtschaffen and Kales (1968) polysomnography scoring norms. The Zeo produces four possible stages: light sleep (Stages 1 and 2 combined), deep sleep (Stages 3 and 4 combined), REM sleep, and wakefulness. For full details of the Zeo, see Shambroom, Fabregas and Johnstone (2012).

Procedure

Overall paradigm timeline

The study was divided into two sessions separated by a 12-hour interval. During the first session, participants first viewed the verbal paired associates (for the baseline time of day memory test) and then the composite scenes (for the memory trade-off task). After completing both incidental encoding tasks, all participants underwent standardized tests to measure mood at time of testing (PANAS) and daytime sleepiness, which took approximately 30 minutes to complete. Participants then continued on to the verbal paired associates cued recall test, which concluded session 1. At the end of first session participants were told that they would return to the lab after 12 hours to complete some ratings. Participants in either 12-hour interval group were asked to keep track of their bedtime and wake time (sleep group) or their activities during the day (wake group). Participants in the sleep group were given Zeo headbands and instructed to wear the headband while they slept. Participants in the wake-interval group were asked not to nap during the 12-hour interval. After the 12-hour interval participants returned to the lab for a surprise recognition test on the different components of all of the composite scenes they had seen in session 1 (for schematic of overall timeline, see Figure 1). The baseline time of day memory test and memory trade-off task will be described in further detail below.

Baseline time of day memory task

Because memory in the memory trade-off task (described in the next section) was tested at different times of the day, a short cued recall task was administered 30 min after encoding to establish baseline performance for declarative stimuli using verbal paired associates. During the encoding period, verbal paired associates were presented sequentially on a Macintosh desktop computer screen using PSYSCOPE X (B 53; Bonatti, 2008). In order to avoid intentional learning, participants were not informed that they would later be tested on the word pairs. Participants were shown a pair of words and instructed to visualize a situation in which the two words would go together. In order to allow for deeper encoding, participants then rated how successful they were in forming an association (e.g., visualizing the two words together) using a Likert-type scale of 1 (extremely unsuccessful) to 5 (extremely successful).

Each trial began with a white fixation cross in the center of the computer screen for 1 second. A word pair was then presented in the center of the computer for 4 seconds during which the participant attempted to visualize the two words together. A 1 to 5 number scale was then presented horizontally at the bottom of the screen with the words “Unsuccessful” and “Successful” as anchors above the numbers 1 and 5 respectively. The scale remained on the screen for 1 second during which participants were asked to rate how successful they were at the association task using the 1-5 number keys on the computer keyboard.

After a 30 minute interval, during which participants completed questionnaires, participants were shown the cue word for each verbal paired associate followed by the first letter of the second word on a computer screen and were asked to report what the second word (the target word) for each pair was. Although participants had an unlimited period of time to complete the cued-recall test, they were instructed to respond as quickly and accurately as possible. Responses were recorded by the experimenter.

Memory trade-off task

Encoding task: Participants were told that they would be viewing photographs of scenes and were instructed to indicate whether they would approach or avoid each scene by making ratings on a 1-5 Likert-type scale (1= move extremely close, 3= stay in same location, and 5= move extremely far), pressing a corresponding key on the computer keyboard. All participants practiced the rating task before the actual experiment, using a separate set of stimuli. The purpose of the approach/avoidance task was to ensure that participants were attending to the composite scene during the encoding phase.

Each encoding trial began with a fixation cross presented for a variable duration of 1 sec, followed by the presentation of a composite scene for 2 sec. Next, a response screen appeared for 6s, during which participants were instructed to make their approachability keyboard rating response. Participants were instructed to view the scene while it was on the screen and to wait until the response screen was presented to make their response. All participants were able to respond within the time allotted. Task instructions emphasized making an accurate rather than a rapid response, and the response screen was always presented for the full 6 seconds, regardless of response reaction time (Figure 3, for diagram of picture encoding trial). Stimulus sets were counterbalanced across runs across participants.

In addition, vigilance-control trials were embedded within the encoding task to provide an objective measure of alertness and vigilance (described in detail in Hu et al., 2006). For each vigilance-control trial, participants saw a number, either a '1' or a '0', instead of a composite scene and were instructed to respond using the corresponding key as quickly as possible.

Recognition task: After a 12-hour delay interval that included either a period of wake or sleep, participants returned for an unannounced recognition memory test. The recognition test was not mentioned during the encoding session, to minimize potential selective rehearsal effects. Participants were told that they would be completing additional ratings. At test, studied items and backgrounds were presented separately and were intermixed together with new item and backgrounds. Forty old (i.e., previously presented) items and 40 old backgrounds from each of the four stimulus categories (a total of 160 old items and 160 old backgrounds) were presented intermixed with 20 new items (i.e., not previously presented) and 20 new backgrounds from each category (a total of 80 new items and 80 new backgrounds). Items were shown against a white background and sizing and orientation was identical to the encoding presentations. All backgrounds were shown without their paired item. Sizing of the backgrounds at retrieval was 1000 x 750 pixels, which was identical to encoding. Participants were instructed to view each item or background and to make a recognition memory judgment using a 1-6 confidence scale (1= definitely new, 2= probably new, 3= maybe new, 4= maybe old, 5= probably old, 6= definitely old). Each item or background was presented for 2 s, followed by a recognition response screen. Participants were allowed an unlimited amount of time to make a response (see Figure 3, for representative retrieval trials). Participants completed a short practice recognition test (using a separate set of items) before the actual recognition test to ensure that participants fully understood the task and the response scale.

Subjective emotional ratings

After the recognition memory test for the memory trade-off task, participants were asked to provide subjective ratings of emotional arousal and distinctiveness for all the objects they had previously seen. Participants were instructed to rate how strong an emotional reaction they had to the object using a Likert scale of 1 (low) to 5 (high). For low arousal ratings, words like calm, relaxed, bored, or sleepy were described the endpoint whereas words like excited, nervous, or wide-awake were used to describe the high arousal endpoint. Participants were then instructed to rate how visually distinctive they found each object using a Likert scale of 1 (not distinctive) to 4 (very distinctive). Participants rated the items they had seen in the original encoding session.

Data Analysis

Cued recall for baseline time of day memory task

To measure baseline memory performance for both the sleep and wake groups, a cued recall task was performed. Cued recall performance was calculated by dividing the number of correct responses by the number of possible correct responses. In order to compare memory performance between the sleep and wake groups an independent student t-test was performed.

Quantifying the memory trade-off

The memory trade-off effect has been defined as the enhancement of memory for emotional items combined with a corresponding decrease in memory for simultaneously presented background stimuli, relative to the corresponding measures for neutral items (Kensinger, Garoff-Eaton, & Schacter, 2007a). The memory trade-off effect for positive, negative, and distinctive items was assessed by comparing corrected recognition memory performance (the proportion of hits minus the proportion of false alarms) for each of these conditions to corrected recognition memory performance in the neutral item condition. The trade-off effect for background scenes was assessed in a similar way, by comparing corrected recognition memory performance between the background scenes that had been paired with items during encoding in each corresponding condition (positive, negative, or distinctive items) and the corresponding memory measure for the backgrounds that had been paired with neutral items during encoding.

To assess recognition memory performance, the proportion of recognition hits was calculated on the basis of correctly recognized items or backgrounds that received recognition confidence responses of ‘4’, ‘5’, and ‘6’, whereas the proportion of false alarms was based on the proportion of new items or backgrounds that received recognition confidence responses of ‘4’, ‘5’, and ‘6’. In an additional analysis high-confidence recognition responses were analyzed separately. In order to calculate high confidence memory, correct confidence responses of ‘5’ and ‘6’ were coded as ‘hits’ and incorrect confidence responses of ‘5’ and ‘6’ were coded as ‘false alarms’.

Calculating the effects of sleep on memory trade-offs

The effect of sleep on memory trade-offs for negative, positive, distinctive, and neutral composite scenes was evaluated with repeated measures analyses of variance

(ANOVAs) with category (negative, positive, distinctiveness, and neutral) and component (item and background) as within-subject factors and interval (sleep and wake) as a between subjects factor. Then, three separate repeated measures ANOVAs were calculate comparing each experimental category to neutral. Effect size was assessed as general eta squared (η_G^2). Interaction effects were further evaluated with planned comparison t-tests.

In order to determine whether there were differences in the magnitude of the memory trade-offs observed between the sleep and wake groups for emotional conditions and distinctiveness, repeated-measures ANOVAs were conducted using difference scores. Difference scores were calculated by subtracting the neutral corrected recognition performance for items and backgrounds from the corrected recognition performance for the items and backgrounds in the three experimental conditions (e.g., difference score for negative items = corrected recognition for negative items – corrected recognition for neutral items). Effect size was assessed as general eta squared (η_G^2). Interaction effects were further evaluated with planned comparison t-tests.

In order to measure the association between sleep and memory performance Pearson correlations were calculated between the total time of sleep, time in light sleep, time in deep sleep, and time in REM sleep, and memory performance.

Subjective arousal and mood ratings for interval groups

In addition to objectively measuring the lack of circadian effects between sleep and interval groups using a cued recall task, independent t-tests were performed on subjective ratings of alertness (as measured by SSS) for the sleep and wake groups.

Finally, in order to verify that differences in mood at the time of testing did not account for differences in emotional memory performance between groups independent t-tests were performed comparing Positive Affect and Negative Affect scores ("I feel this way now" scale was used) for the different groups.

Results

An alpha of less than 0.05 was set a priori for all statistical analyses. Due to the relatively small sample size, P values between 0.05 and 0.10 were considered to be 'marginally significant' and will be interpreted tentatively as this range increases the likelihood of a false positive.

Effect Of Time Of Day On Sleep-interval And Wake-interval Conditions

In order to test whether diurnal differences were responsible for any observed differences in memory performance between the sleep-interval and wake-interval groups we measured subjective alertness using the Stanford Sleepiness Scale and found no significant differences between groups (M=2.66, SEM=0.17 vs. M= 2.53, SEM=0.20, p= 0.62). In addition, as an objective measure of vigilance, reaction times for alertness-control trials embedded within the encoding task showed no significant difference between sleep (M=1.37, SEM=0.12) and wake (M=1.13, SEM=0.05) groups, although the difference between groups was marginally significant; $t(36)=1.97$, p=0.06.

Some evidence suggests that there are diurnal differences in mood (Boivin et al., 1997), specifically that negative mood increases as the day progresses. Therefore, in order to ensure that any enhancement in emotional performance was not a result in differences in subjective mood at the time of testing Negative Affect and Positive Affect scores were calculated and compared using an independent means t-test. There were no differences between the sleep and wake groups for Negative Affect (M= 14.79, SEM=

0.90 vs. *M*= 14.58*, SEM*= 1.07, *p*= 0.90) and Positive Affect (*M*= 24.74*, SEM*= 1.88 vs. *M*= 19.05*, SEM*= 1.52, *p*= 0.06), although it was marginally significant in the case of Positive Affect.

In order to determine that there were no time-of-day effects on encoding processes, we first examined whether time of day effects influenced memory performance in a separate short (30 min) delay cued recall task and found no difference between sleep and wake groups (*M*= 0.61, *SEM*= 0.04 vs. *M*= 0.63, *SEM*= 0.04, *p*= 0.79). However, as this was a between-groups test and did not measure any circadian differences within each participant we cannot completely eliminate the time of day effects with group.

Sleep vs. Wake Memory Trade-Off Comparisons

Full descriptions of hits (correct 'old' response), false alarms (incorrect 'old' response), and corrected recognition performance for all items and backgrounds for sleep and wake groups are listed in Table 3.

Analyzing differences in memory trade-offs between sleep and wake group

To assess whether memory trade-offs were stronger after sleeping for emotional and distinctive scenes, relative to the neutral scenes, a repeated-measures ANOVA with factors of interval (sleep vs. wake) as a between-subjects factor, and factors of category (negative, positive, distinctive, neutral) and scene component (item vs. background) as within-subjects factors was conducted. There was no significant main effect for interval $F(1, 36) = 0.82$, $p = 0.37$, $\eta_G^2 = 0.02$ indicating that there was no overall difference between sleep and wake groups for memory performance. There was, however, a significant main effect for category $F(3, 108) = 5.72$, $p = 0.001$, $\eta_G^2 = 0.14$ and scene component $F(1, 36) = 183.52$, $p < 0.005$, $\eta_G^2 = 0.83$. Additionally, there was a significant interaction between category and scene component *F*(3, 108) = 15.62, $p < 0.005$, $\eta_G^2 = 0.30$ indicating that there were memory trade-offs overall. However, there were no significant interactions between interval and category *F*(3, 108) = 0.50, $p = 0.68$, $\eta_G^2 = 0.004$ and interval and component *F*(1, 36) = .59, $p = 0.45$, $\eta_G^2 = 0.002$, and no three way interaction between interval, category, and component *F*(3, 108) = .50, $p = 0.68$, $\eta_G^2 = 0.01$ indicating that there were no differences in memory trade-offs between sleep and wake interval groups (see Figures 4, 5, and 6 for group comparisons for negative, positive, and distinctive scenes respectively).

Based on the hypothesis that sleep would increase memory trade-offs for distinctive and emotional scenes we examined the effect of sleep on memory trade-offs for emotional and distinctive scenes in three separate repeated-measures ANOVAs with category (emotional or distinctive category, neutral) and component (item, background). For each of these repeated-measures ANOVAs, interval (sleep vs. wake) was a between-subjects factor. As with the omnibus repeated-measures ANOVA, there were overall memory trade-offs for negative, positive, and distinctive scenes, which did not differ between sleep and wake groups. Full descriptions of these analyses can be found in Appendix 3.

Although there was no difference in memory trade-off performance between sleep and wake groups, significant interactions between category and scene component indicated that there were overall memory trade-offs, for emotional and distinctive scenes. Planned-comparison paired t-tests revealed that corrected recognition for negative items was significantly higher than neutral items; $t(37) = 6.21$, $p < 0.005$, as were positive items; $t(37) = 5.62$, $p < 0.005$ and distinctive items; $t(37) = 6.65$, $p < 0.005$. Paired t-tests also confirmed that corrected recognition for backgrounds paired with negative items was significantly lower than backgrounds paired with neutral items; *t*(37) = -2.82, *p* = 0.01, as were backgrounds paired with distinctive items; *t*(37) = -3.27, *p* = 0.002. Backgrounds paired with positive items, however, were not significantly lower than backgrounds paired with neutral items; *t*(37) = 0.35, *p* = 0.73. In sum, there were overall memory trade-offs for negative and distinctive scenes (due to both enhanced memory for negative and distinctive items and reduced memory for negative and distinctive backgrounds) after a 12-hour interval. However, this result did not differ based on whether the participant had sleep or not during the 12-hour interval period.

Differences in the magnitude of memory trade-off effects between sleep and wake groups: As there were no differences in memory trade-offs between sleep and wake groups, it is unlikely that there would be differences in the magnitude of a memory trade-off for either emotional or distinctive scenes after a interval that included either sleep or wakefulness. As a result, analyses investigating possible differences in magnitude of memory trade-offs between sleep and wake group will not be discussed here. For reference, a description of such analyses are described in Appendix 3 and confirm that there were no differences in the magnitude of memory trade-off effects between sleep and wake groups.

Analyzing differences in memory trade-offs for high confidence responses between sleep and wake group

In addition to analyses of overall recognition performance, recognition performance for high-confidence responses was also analyzed (e.g., corrected recognition calculated using hits and false alarms corresponding to “5” and “6” confidence responses). This was in order to investigate whether there were differences in memory trade-off performance between groups based on how confident participants were during recognition, which may reflect recollection-type memory as “5” and “6” responses may reflect instances when participants remember additional contextual information to respond more confidently (Kim & Cabeza, 2007). Alternatively it could reflect how accurate they were after sleep as instances of guessing (“4” maybe responses) were taken out. However, high-confidence analyses showed an identical pattern as was described for general recognition performance above and will not be further discussed here. Descriptions of analyses can be found in Appendix 4. Memory performance for items and backgrounds for high-confidence responses is listed in Table 4.

Accounting for differences in vigilance and daytime sleepiness

As there were potential differences between the sleep-interval and wake-interval groups regarding subjective daytime sleepiness (measured by the Epworth Sleepiness Scale) and objective vigilance (measured by reaction time during embedded alertness trials in encoding task), the above analyses were conducted on an equated sample for subjective daytime sleepiness and objective vigilance. However, equating the samples did not change the above findings and thus, the remaining analyses will be conducted with the entire data set to increase statistical power.

Correlation Between Memory Performance And Sleep Measures

In addition to examining whether sleep in itself would benefit subsequent memory performance, the effect of different components of sleep on subsequent memory performance was also investigated. Although sleep data was not collected using polysomnography (PSG)—a multi-parametric test which measures cortical brain activity, eye movements, and muscle movements, which is considered the gold standard of sleep measurement (Kushida et al., 2005)—participants assigned to the sleep-interval group provided journals of their sleep behavior in between the encoding and memory sessions. Additionally, participants wore wireless monitoring devices (Zeo), which recorded some preliminary sleep measures including light sleep, deep sleep, and rapid eye-movement (REM) sleep (breakdown of sleep components can be found in Table 5). Pearson correlations were conducted to measure the relationship between memory performance for item and backgrounds in each of the experimental categories (negative, positive, distinctive, and neutral) and sleep measures (total time asleep, light sleep, deep sleep, and REM).

Correlation with time spent asleep

Pearson correlations measuring the relation between the amount of post-learning sleep (measured by sleep journals) and subsequent memory performance showed weak to no relation with most of the categories (negative items, positive items, distinctive items, neutral items, negative backgrounds, positive backgrounds, and neutral backgrounds), which are listed in Table 6. However there was a positive relation that was marginally significant for sleep duration and corrected recognition memory for backgrounds paired with distinctive items $r(19) = 0.42$, $p=0.08$. There was no relation between amount of sleep and high confidence subsequent memory performance for any of the categories.

Correlations with Zeo calculated sleep stages

Pearson correlations were also calculated to measure the relation between specific sleep measures (minutes in light sleep, deep sleep, and REM sleep) and subsequent memory performance for all categories and components. Previous research suggests that deep sleep stages (combination of Stages 3 and 4 in Zeo) play a role in episodic memory consolidation (Gais & Born, 2004b), whereas REM has been implicated in emotional memory consolidation (Wagner et al., 2001). Three of the nineteen participants in the sleep-interval group where missing Zeo sleep stage data[3]. As a result of the missing Zeo sleep stage data, Pearson correlations were conducted on the sixteen participants with sleep stage data. With respect to light sleep, deep sleep, and REM sleep there were no significant correlations. All correlations between sleep measures and memory performance are listed in Table 6.

Discussion

The main goal of the current study was to investigate the effect of a full night of sleep on consolidation of negatively arousing, positively arousing, distinctive (but emotionally neutral) scenes. With that objective, participants viewed pictures of scenes consisting of a target item (either negative, positive, neutral, or distinctive but emotional neutral) superimposed over neutral indoor and outdoor background scenes. After a 12 hour interval, during which participants went home and slept or experienced an equivalent period of daytime wakefulness, participants returned to the lab for an unannounced recognition test where they were tested on the central items and backgrounds separately in order to assess memory for each of these two elements. Previous research has suggested—when comparing negative and neutral scenes—that the magnitude of memory trade-offs is enhanced after a full night of sleep (Payne et al.,

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[3] The reason for the missing data is unclear although there are several possible explanations. The primary explanation for missing data is likely participant error in downloading the data and, more specifically, in failing to properly place the headband in the Zeo station dock before unplugging the clock device, which would prevent data from being saved. Although participants were instructed, both verbally and with written instructions, to place the headband on the station dock it is possible that three of the participants did not do this. Other explanations include a poor wireless connection between the headband and base station, SD card malfunction, and battery failure (M. Scullin, personal communication, July 5, 2013)

2008). Moreover, we previously demonstrated that negative and positive emotion, and distinctiveness were factors which could elicit memory trade-offs of the same magnitude (Campanella & Hamann, in preparationa, in preparationb). Thus, it was predicted that memory trade-offs for negative, positive, and distinctive scenes would be enhanced after a full night of sleep. However, contrary to what was hypothesized, there was no difference in the magnitude of the memory trade-off between sleep and wake interval groups. Overall recognition performance was equivalent between the two interval groups. There was, however, an interesting non-significant correlation between sleep duration, collected with sleep journals, and corrected recognition performance. To be specific, there was a marginal positive correlation (p= 0.08) between sleep duration and corrected recognition performance for backgrounds paired with distinctive items. The present findings suggest that although there may not be an apparent difference in memory performance after sleep, it is possible that the amount of sleep a person gets may impact that information they remember. However, all of the correlations were not significant and as such it is difficult to make clear interpretations on the role that sleep may play on memory trade-offs. Any interpretation on the correlations, which might be considered marginally significant, must be approached with caution, as there is a higher chance of false alarms. It does suggest, however, that further investigation with larger sample sizes might be worthwhile in determining whether sleep duration, as well as specific sleep components, such a role in selective memory consolidation. However, before delving into the interpretation for why certain aspects of sleep may potentially selectively consolidate emotional, distinctive, and neutral memory the unexpected finding of no behavioral difference in recognition performance between sleep and wake interval groups will be discussed.

Explanations For The Lack Of A Sleep Effect For Memory Trade-Offs

The present study used a similar memory trade-off paradigm, which was previously utilized by Kensinger and colleagues for both sleep and no sleep manipulations (Bennion et al., 2013; Payne et al., 2008; Kensinger et al., 2007; Waring & Kensinger, 2009). The primary difference between the current study and previous memory trade-off studies investigating the effects of sleep is that the current study included two additional categorical conditions, specifically positive emotion and distinctiveness, whereas previous studies only compared negative emotion to neutral. Previous findings demonstrated an enhancement in the emotion induced memory trade-off effect, which is when central and salient aspects of emotional episodic scenes are remembered at the expense of background, neutral information, for individuals who slept in the interval between the learning session and the memory test (Payne et al., 2008). In the current study there was an overall memory trade-off effect observed for negative, positive, and distinctive scenes, which was consistent with previous work in the laboratory (Campanella & Hamann, in preparationa); however, the magnitude of the trade-off was equivalent between sleep and wake interval groups.

One possible explanation for the lack of difference between groups could be potential diurnal differences between groups, specifically systematic differences related to the time of day that participants were tested could cause participants in the wake-interval group to perform better, thus washing out any beneficial effect of sleep. Performance and alertness was measured in three different ways: first participants were given questionnaire designed to measure subjective alertness during both the encoding and retrieval sessions. Second, participants were given a cued-recall memory test during the encoding session on unrelated verbal paired associates to determine baseline memory performance. Finally, vigilance RT trials were randomly embedded within the encoding task during which participants saw one of two numbers and had to press the corresponding key as quickly as possible. There were no differences in subjective ratings of alertness between the two interval groups. In addition, there was no difference in memory performance for the baseline cued recall task suggesting that any differences, or lack thereof, should not account for differences in baseline alertness and cognitive functioning. There was, however, a systematic difference in vigilance between with groups. Specifically, participants in the wake group were marginally faster ($p= 0.06$) to respond to the vigilance trials suggesting they were more alert and engaged during the encoding task. Thus, it is possible that although wake-interval participants may not have better overall memory functioning as measured by the cued-recall memory test, they may have been paying more attention to the composite scene than the participants in the sleep group resulting in better overall memory for that task.

One possible explanation for the difference in baseline vigilance during encoding may be that participants in the sleep interval group were—potentially—more sleep deprived than participants in the wake interval group. Although participants in both groups showed no differences in the amount of sleep they got prior to coming in for the study, participants in the sleep group reported marginally higher levels of daytime sleepiness ($p= 0.09$) (measured with the Epworth Sleepiness Questionnaire). Memory performance is significantly disrupted after a night of pre-training sleep deprivation

(Drummond et al., 2000; Harrison & Horne, 2000; Morris, Williams, & Lubin, 1960; Yoo, Hu, Gujar, Jolesz, & Walker, 2007). In addition, individuals are worse at judging their performance and state of being after a night of sleep deprivation (Harrison & Horne, 2000). This explanation, however, seems unlikely for the current study. When slow responders for the vigilance task or individuals with excessively high Epworth scores (<20) were removed (3 participants for each group), there was no change in memory performance for the memory trade-off task between groups. This suggests that the effect of differences in vigilance and daytime sleepiness between groups on subsequent memory performance for the composite scenes was negligible, thus discounting this explanation.

Another explanation could be related to the memory task used in the current study. Increasing evidence suggests that sleep benefits on memory performance are strongest for intentional memory tests (Diekelmann et al., 2012; Diekelmann & Born, 2010; Rauchs et al., 2011; Saletin et al., 2011; Wilhelm et al., 2011). The current study, however, used an incidental memory paradigm, which might explain why there is no difference between sleep and wake group. However, emotion, which by nature makes stimuli highly salient, may make incidental learning of emotional information intentional (Wilhelm et al., 2011) suggesting that emotional stimuli would be enhanced in a similar fashion to stimuli learned through intentional encoding. Related to differences in memory task, strongest benefits in memory are often seen in recall memory paradigms compared to recognition paradigms (Diekelmann, Wilhelm, & Born, 2009) suggesting that the lack of enhancement of memory after sleep in the current paradigm may be due to the fact that recognition memory is being tested. However, previous studies investigating the effect of sleep on memory trade-offs have also used a recognition paradigm and seen sleep benefits (Payne et al., 2008) suggesting that the type of memory test is unlikely to be the cause in the lack of enhancement after sleep in this particular experiment.

Finally, a possible explanation for the absence of a preferential sleep effect on memory may be that in this particular situation salient information may be reactivated during both sleep and states of wakefulness. Although a majority of studies show a selective reactivation of salient information during sleep (Fischer & Born, 2009; Rauchs et al., 2011; Wilhelm et al., 2011), some evidence suggests that certain salient information may also be reactivated during wakefulness. Animal studies have demonstrated that in the context of rewarded learning, wakefulness may also contribute to consolidation of salient memories. More specifically, in a spatial navigation task, rewarded outcomes enhanced waking reactivation of paths associated with reward location during learning (Singer & Frank, 2009). Moreover, the amount of reactivation of goal-related patterns predicted later memory performance, regardless of whether reactivation occurred during the acquisition phase or the subsequent rest phase, suggesting that both online and offline reactivation can strengthen memory (Dupret, O'Neill, Pleydell-Bouverie, & Csicsvari, 2010). Human studies show a similar pattern with high-value information being reactivated during both periods of wakefulness and sleep, whereas low-value information was reactivated solely during sleep (Oudiette et al., 2013), suggesting that both periods wakefulness and sleep are important for memory consolidation. Specifically that reactivation during wakefulness may help strengthen individual salient memories, whereas sleep may also help strengthen individual memories while also linking categorically related memories together. Conversely, other studies suggest that highly salient (Wilhelm et al., 2011), rewarded (Fischer & Born, 2009), and highly emotional (Payne et al., 2008) are only selectively reactivated and consolidated during sleep. Thus it appears that what information is selectively reactivated during sleep, versus during a period of wakefulness may be dependent on the paradigm being used. In the context of the current study, the paradigm differed from previous memory trade-off paradigms by including 4 categories for composite scenes (negative arousing, positively arousing, distinctive, and neutral), whereas previous memory trade-off studies investigating the effects of sleep have only compared two categories (negatively arousing or neutral). It is possible that the addition of two categories may change how participants perceived the scenes and processed them. Although this was not tested in the current study, one could speculate that participants spent more time elaborating on the inter-item similarities between the four different groups, which could in turn lead to increased reactivation during periods of wakefulness. This increased elaboration during wakefulness would subsequently be reflected in enhanced memory performance in the wake group. Further experimentation investigating how participants perceive the different scenes is needed to verify that saliency may change with context and lead to differential reactivation during periods of sleep and wakefulness.

Correlations Between Corrected Recognition Performance And Sleep Measures

Although there were no observed differences in memory performance between sleep and wake interval groups it is impossible to rule out the possibility that in the current experiment, sleep produced a memory benefit too small to measure relative to between subject variability in memory. However, in the context of the current study, a secondary goal was to investigate the role that different components of sleep may have on subsequent memory performance, which could begin to address whether emotional and distinctive memories are consolidated during sleep through the same mechanism. Total sleep duration was collected with sleep journals and duration in light sleep (which corresponds to the first two stages of sleep), deep sleep (which corresponds to SWS), and rapid eye movement (REM) sleep were collected with Zeo wireless devices. Problems related to subject size and power become relevant in this section as many of the correlations that will be discussed were not significant despite demonstrating moderate to strong relations between sleep measures and memory performance based on Pearson R values. Only correlations, which might be classified as approaching significance based on p-values of 0.10 or less will be discussed below and should therefore be interpreted with caution, as there is an increased risk of false positives.

Overall, some aspects of sleep may weakly influence different components of memory. To be specific, there was a positive non-significant relation between total sleep duration and corrected recognition for backgrounds paired with distinctive items. Previous research has demonstrated that there is a relationship between the amount of sleep an individual gets and subsequent memory performance through either an all or nothing manner where a minimum amount of sleep is needed to benefit memory, or in a dose-dependent manner where benefits on memory increase the longer an individual sleep (for review, see Diekelmann et al., 2009). The current findings might be consistent with the second view as enhancements in memory for distinctive backgrounds increased as individuals spent more time sleeping in the interval after learning. However as the measurement of sleep duration does not describe any special physiological property of sleep, but instead the passage of time, it is also possible that the relationship between sleep duration and memory performance reflects a passage of time during which sleep passively protects information from interference and therefore does not actively influence memory consolidation.

In order to determine whether sleep duration accurately measures sleep's *active* role in episodic memory consolidation for distinctive and emotional scenes, it is also important to investigate the different stages that make up a full night of sleep. Previous evidence suggests that SWS sleep plays an important role in strengthening episodic memories (Alger et al., 2012; Diekelmann et al., 2012; Gais & Born, 2004b; Peigneux et al., 2004; Rasch et al., 2007), whereas REM sleep appears to play a role emotional processing (Groch et al., 2013; Nishida et al., 2009; Sterpenich et al., 2009; Wagner et al., 2001). In the current study, there was no positive correlation between deep sleep (Zeo correlate with SWS) and increased memory function and therefore there is no evidence of SWS playing a role in strengthening episodic memory. There was also no evidence of REM sleep enhancing memory performance. Thus, based on the current evidence, it is unclear if sleep plays an active role in memory consolidation of the composite scenes.

It is important to keep in mind, however, that the current study used Zeo wireless devices, which are not as accurate in measuring sleep stages as polysomnography (the gold standard of sleep measurement). For example, in the current study, the Zeo calculated that on average participants spend 56% of the night in deep sleep (see Table 5), which is considerable higher than the 25% that has typically been recorded with polysomnography (Carskadon et al., 2000). Moreover, Zeo wireless devices are unable to record more fine-tuned physiological features of different sleep, such as sleep spindles, theta activity, and delta activity. As a result, the current measures may not be sensitive enough to detect benefits for more salient information, such highly emotional or distinctive information. Although there was a not-significant benefit for the time spent sleeping and memory for backgrounds paired with distinctive items it is unclear whether this benefit was a result of some component of sleep, or merely passive protection of distinctive information during sleep. Emotional information, on the other hand, appeared to receive no particular benefit from sleep, although again it is unclear whether the current sleep measurements were not sensitive enough to detect effects. A study with a polysomnography-recorded sleep session and a larger sample size may be able to better answer these questions.

What is interesting to note, however, is that, overall, the current study shows weak evidence of sleep duration mediating consolidation of “low-value” information (i.e., background and neutral information). Specifically that the current study showed a correlation between sleep duration, and memory performance for background information. Although contradictory to previous findings (Payne et al., 2008; Payne & Kensinger, 2010; Wilhelm et al., 2011), which show that sleep preferentially consolidates highly salient information—which would be considered of higher evolutionary value—there is increasing evidence which suggests that under certain conditions there is a greater sleep benefit for weakly encoded memories (Drosopoulos, Schulze, Fischer, & Born, 2007; Kuriyama, Stickgold, & Walker, 2004). As background information attracts fewer attentional and cognitive resources (Easterbrook, 1959; Reisberg & Heuer, 2004) it seems reasonable to assume that this information is more weakly encoded and may therefore preferentially benefit from memory processing during sleep. In support of this view is evidence that sleep may play a greater role in reactivating “low-value” information (Oudiette et al., 2013) or, conversely, globally enhance salient behavior with no preference to high or low value items (Baran, Daniels, & Spencer, 2013). A study with polysomnography-recorded sleep may be able to test this intriguing hypothesis.

Conclusions

In summary, one goal of the current study was to investigate the effect of a full night of sleep on consolidation of negatively arousing, positively arousing, distinctive (but emotionally neutral) scenes. It was hypothesized that memory trade-offs for emotional and distinctive composite scenes would be enhanced after a full night of sleep, compared to an equivalent period of daytime wakefulness. However, contrary to what was hypothesized, there was no selective enhancement in memory trade-offs for either emotional or distinctive scenes after sleep. In fact, behaviorally there appeared to be no benefit of sleep on memory performance for any component of the scenes. There were, however, a non-significant correlation (which may not be significant due to a lack of power) between sleep duration and memory for backgrounds paired with distinctive items. Thus, it appears that there may be a selective benefit of sleep for more weakly encoded information, which is consistent with some previous literature. Further research is needed to identify the mechanism by which sleep selectively consolidates these memories. Nevertheless, the current evidence offers tentative suggestions that in certain contexts sleep may play a role in consolidating weakly encoded information and demonstrates a need to further elucidate the mechanisms by which sleep selectively consolidates information.

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Tables

Table 1

Demographic information for Sleep-Interval and Wake-Interval Conditions

	Group				
	Sleep		Wake		Difference
Test	*M*	*SEM*	*M*	*SEM*	*p*
Age	19.47	0.25	19.47	0.24	0.53
Average Sleep	8.12	0.22	7.86	0.16	0.35
Epworth Score	9.05	0.79	7.05	0.81	0.09
Stanford Sleepiness Scale	2.66	0.17	2.53	0.20	0.62
PANAS					
Positive Affect	24.74	1.88	19.05	1.52	0.06
Negative Affect	14.79	0.90	14.58	1.08	0.90

Table 2

Mean subjective arousal and distinctiveness ratings for all items

	Rating			
	Arousal		Distinctiveness	
Category	*M*	*SEM*	*M*	*SEM*
Negative	2.71	0.13	2.05	0.08
Positive	2.61	0.16	1.41	0.11
Distinctiveness	2.32	0.15	3.83	0.09
Neutral	1.90	0.07	1.57	0.08

Note: Subjective arousal and distinctiveness ratings were calculated on a 5 point Likert-scale (1= low to 5= high). For arousal ratings all categories differed from each other at $p < 0.005$ except for arousal between negative and positive items and arousal between positive and distinctive items. For distinctive ratings, all categories differed from each other at $p < 0.005$ except for positive and neutral items.

Table 3

Recognition Performance for Sleep and Wake Interval Groups

	Group			
	Sleep-interval (N=19)		Wake-interval (N=19)	
Memory Type	*M*	*SEM*	*M*	*SEM*
Hits for Items				
Negative	0.90	0.02	0.87	0.03
Positive	0.83	0.03	0.83	0.03
Distinctive	0.81	0.03	0.82	0.02
Neutral	0.76	0.04	0.77	0.03
False Alarms for Items				
Negative	0.23	0.04	0.18	0.03
Positive	0.19	0.03	0.18	0.03
Distinctive	0.15	0.03	0.20	0.03
Neutral	0.24	0.04	0.26	0.03
Corrected Recognition for Items				
Negative	0.67	0.05	0.68	0.04
Positive	0.64	0.04	0.65	0.04
Distinctive	0.67	0.05	0.63	0.03
Neutral	0.52	0.05	0.51	0.03
Hits for Backgrounds				
Negative	0.50	0.03	0.47	0.03
Positive	0.58	0.03	0.53	0.04
Distinctive	0.45	0.03	0.42	0.03
Neutral	0.55	0.03	0.52	0.04
False Alarms for Background				
Negative	0.28	0.04	0.28	0.04
Positive	0.25	0.04	0.27	0.04
Distinctive	0.25	0.04	0.24	0.04
Neutral	0.24	0.04	0.28	0.03
Corrected Recognition for Backgrounds				
Negative	0.23	0.03	0.18	0.04
Positive	0.33	0.04	0.26	0.04
Distinctive	0.20	0.03	0.18	0.04
Neutral	0.32	0.04	0.25	0.04

Note. Corrected recognition performance was calculated by subtracting proportion of false alarms from proportion of hits. Backgrounds were always neutral and are designated to each experimental category (negative, positive, distinctive, and neutral) by the central item that was originally paired with that background.

Table 4

Recognition Performance for High Confidence Sleep and Wake Interval Groups

	Group			
	Sleep-interval (N=19)		Wake-interval (N=18)	
Memory Type	*M*	*SEM*	*M*	*SEM*
Hits for Items				
Negative	0.84	0.03	0.80	0.04
Positive	0.75	0.04	0.76	0.04
Distinctive	0.75	0.04	0.74	0.03
Neutral	0.65	0.05	0.66	0.04
False Alarms for Items				
Negative	0.17	0.03	0.10	0.02
Positive	0.10	0.02	0.08	0.02
Distinctive	0.07	0.02	0.10	0.02
Neutral	0.11	0.02	0.15	0.02
Corrected Recognition for Items				
Negative	0.67	0.03	0.70	0.04
Positive	0.65	0.04	0.67	0.04
Distinctive	0.68	0.05	0.64	0.03
Neutral	0.54	0.05	0.51	0.03
Hits for Backgrounds				
Negative	0.33	0.03	0.33	0.03
Positive	0.43	0.03	0.39	0.04
Distinctive	0.29	0.03	0.28	0.03
Neutral	0.39	0.03	0.38	0.04
False Alarms for Background				
Negative	0.11	0.02	0.14	0.03
Positive	0.09	0.02	0.13	0.02
Distinctive	0.12	0.03	0.13	0.02
Neutral	0.09	0.02	0.11	0.02
Corrected Recognition for Backgrounds				
Negative	0.22	0.03	0.19	0.03
Positive	0.34	0.03	0.26	0.04
Distinctive	0.17	0.03	0.16	0.03
Neutral	0.30	0.03	0.27	0.04

Note. Corrected recognition performance was calculated by subtracting proportion of false alarms from proportion of hits. Backgrounds were always neutral and are designated to each experimental category (negative, positive, distinctive, and neutral) by the central item that was originally paired with that background.

Table 5

Description of Zeo Sleep Measures in Sleep Group

Zeo Data (N =16)	*M*	*SEM*
Total Time Asleep (min)	352.81	19.26
Sleep Latency (min)	22.75	5.01
Awakenings	2.69	0.85
Time in Wake (min)	13.13	7.64
Time in Light Sleep (min)	206.88	17.04
Time in Deep Sleep (min)	77.25	5.68
Time in REM Sleep (min)	68.81	8.46
Wake (%)	0.03	2.00
Light Sleep (%)	0.19	2.00
Deep Sleep (%)	0.56	2.00
REM Sleep (%)	0.22	2.00

Table 6

Correlations between sleep measures and memory performance

	Time Asleep (N=19)	**Time in Light Sleep (N=16)**	**Time in Deep Sleep (N=16)**	**Time in REM Sleep (N=16)**
Negative Objects	-.252	-.325	.009	.213
Positive Objects	.162	.144	.218	.195
Distinctive Objects	-.114	-.232	.065	.352
Neutral Objects	-.030	-.252	.126	.400
Negative Backgrounds	-.258	-.321	-.391	.056
Positive Backgrounds	.133	-.103	.060	.393
Distinctive Backgrounds	**.417***	.131	-.174	.316
Neutral Backgrounds	-.167	-.086	.053	.069

Note: * denotes $p < 0.10$

Figures

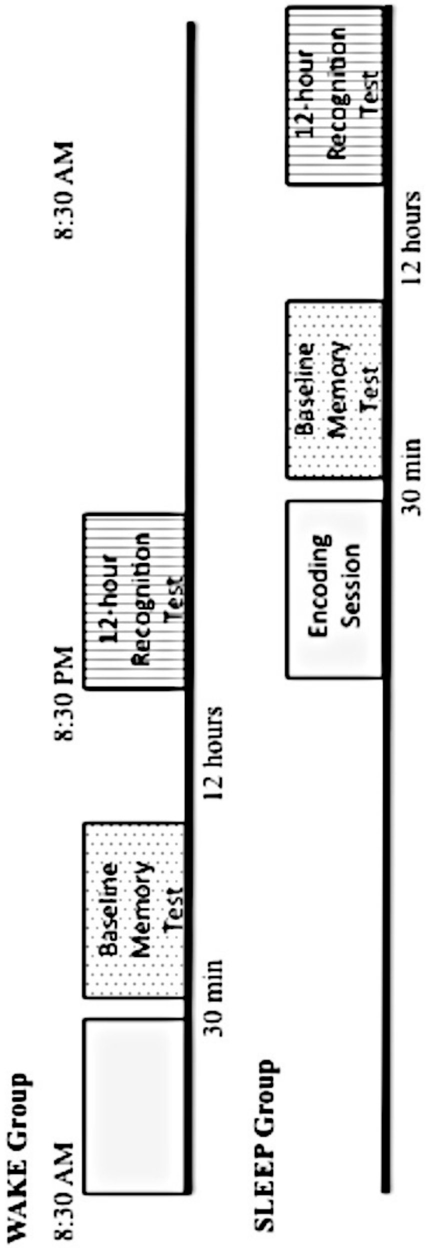

Figure 1: Overall Overnight Paradigm. Baseline Memory Test indicates short cued recall test on verbal paired associates, which was used to assess baseline time of day memory performance. Recognition test refers to recognition test of items and backgrounds, which made up composite scenes

Negative **Positive**

Distinctive **Neutral**

Figure 2: Example of a composite scene from each category. Reflects four different counterbalancing lists. It is important to note that each participant only saw each background once during the encoding session.

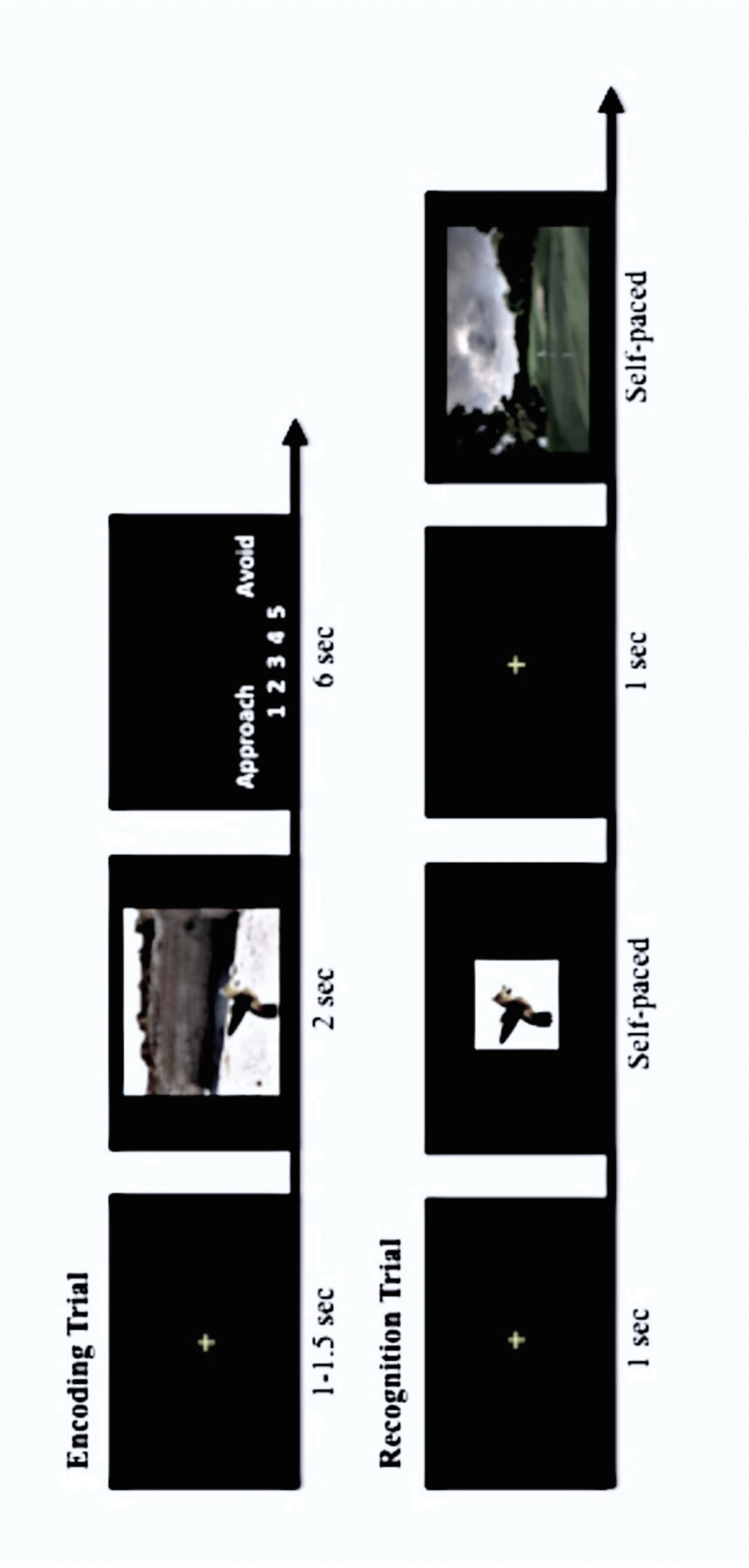

Figure 3: Example of Encoding and Recognition Trials. For recognition trial, there is an example of an OLD item and a NEW background. During recognition trial, participants were instructed to mark their responses on a 1-6 confidence scale (1 = Definitely New, 2 = Probably New, 3 = Maybe New, 4 = Maybe Old, 5 = Probably Old, 6 = Definitely Old)

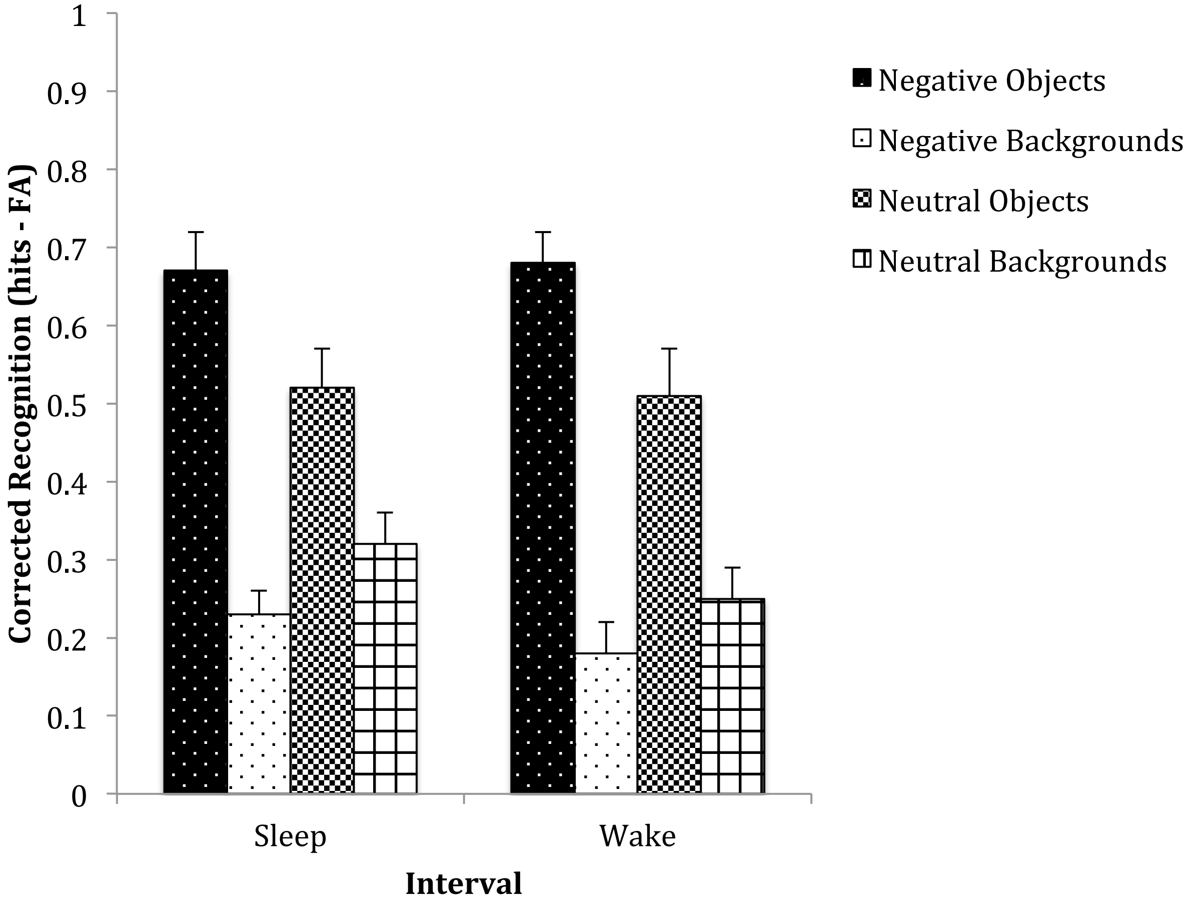

Figure 4: Memory trade-off performance for negative scenes for sleep-interval and wake-interval conditions.

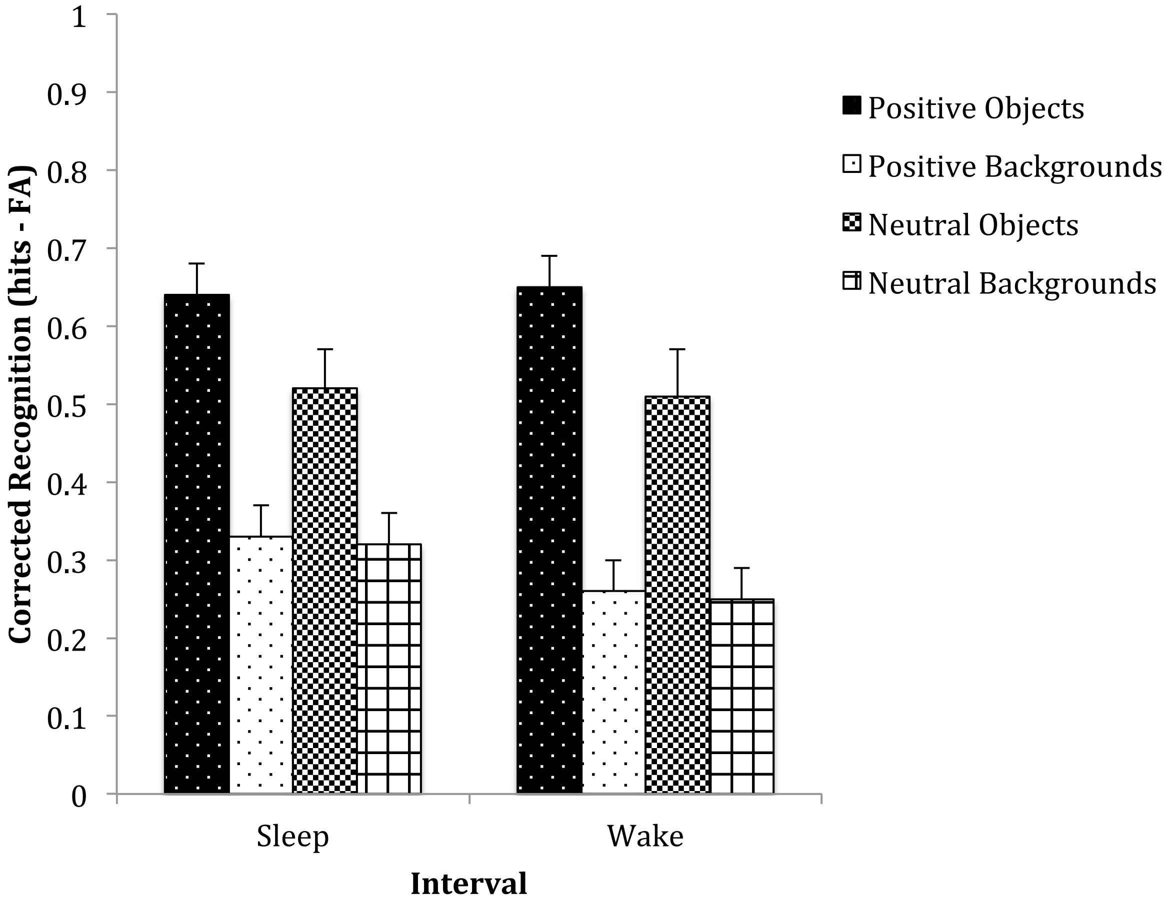

Figure 5: Memory trade-off performance for positive scenes for sleep-interval and wake-interval conditions.

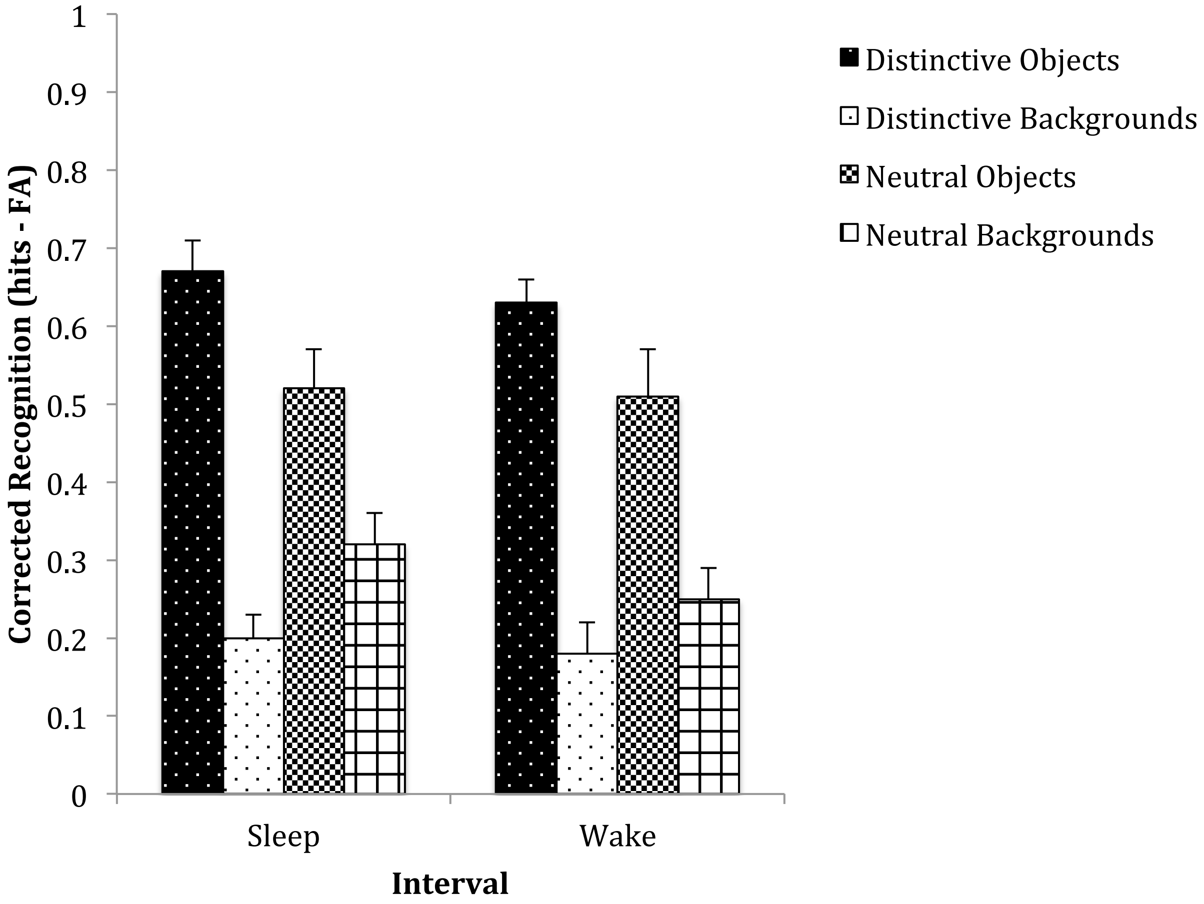

Figure 6: Memory trade-off performance for distinctive scenes for sleep-interval and wake-interval conditions.

Appendix 1

Verbal Paired Associate Lists for Baseline Memory Test. Participants saw one of the two lists.

List 1		***List 2***	
school	blackboard	rider	switch
tower	bell	fire	smoke
sea	tide	animal	fox
family	marriage	road	car
newspaper	interview	weaver	troubles
sonata	joy	flakes	rescue
banner	camp	rein	turn
tendency	increment	mission	messenger
mother	child	furniture	chair
insect	caterpillar	body	blood
river	ship	army	admiral
coast	beach	friend	loyalty
gun	bullet	bird	lark
blacksmith	metal	celebration	alcohol
home	room	reptile	frog
building	hall	grain	oats
rain	flood	joint	knuckle
avenue	tree	artist	painting
decency	truth	statement	doubt
decree	decision	revolt	policeman
diamond	hardness	alliance	betrayal
result	effect	event	incident
occupation	doctor	factory	foreman
book	story	plant	leaf
attack	operation	tenant	rent
cat	soul	commercial	candy
doll	cradle	giant	club
episode	happiness	trip	map
railroad	steam	mountain	boulder
kitchen	pot	ruler	palace
countryside	swamp	play	drama
musician	pianist	illness	doctor
industry	factory	church	heaven
clothing	scarf	infection	bacteria
car	headlight	university	semester
prison	gangster	underworld	crime
bouquet	blossom	instrument	bagpipes
bottle	toast	glacier	avalanche
group	person	idea	proverb

Appendix 2

Example of Epworth Sleepiness Scale (Johns, 1991)

Epworth Sleepiness Scale

How likely are you to doze off or fall asleep in the following situations, in contrast to just feeling tired? This refers to your usual way of life in recent times. Even if you have not done some of these things recently, try to work out how they would have affected you. Use the following scale to choose the **most appropriate number** for each situation

0 = would **never** doze
1 = **slight** chance of dozing
2 = **moderate** chance of dozing
3 = **high** chance of dozing

Situation *Chance of Dozing*

Sitting and reading…………………………………………______________________

Watching TV……………………………………………… ______________________

Sitting, inactive, in a public place (e.g., a theater or a

meeting)…………………………….…………………… ______________________

As a passenger in a car for an hour without a

break……………………………………………….………______________________

Lying down to rest in the afternoon when circumstances

permit…………………………………………………..……______________________

Sitting and talking with someone…………………………….______________________

Sitting quietly after a lunch without alcohol…………………______________________

In a car, while stopped for a few minutes in traffic…………..______________________

Example of Stanford Sleepiness Scale (Hoddes et al., 1972)

Stanford Sleepiness Scale

Instructions: Please rate how alert you feel right now by circling one of the options:

Degree of Sleepiness	**Scale Rating**
Feeling active, vital, alert, or wide awake	1
Functioning at high levels, but not at peak; able to concentrate	2
Awake, but relaxed; responsive but not fully alert	3
Somewhat foggy, let down	4
Foggy; losing interest in remaining awake; slowed down	5
Sleepy, woozy, fighting sleep; prefer to lie down	6
No longer fighting sleep, sleep onset soon; having dream-like thoughts	7

Example of Positive Affect Negative Affect Scale (PANAS) (Watson et al., 1988)

This scale consists of a number of words that describe different feelings and emotions. Read each item and then mark the appropriate answer in the space next to that word. Indicate to what extent you feel this way **right now**, that is, at the present moment. Use the following scale to record your answers:

1	**2**	**3**	**4**	**5**
very slightly or not at all	a little	moderately	quit e a bit	extremely

___ interested

___ distressed

___ excited

___ upset

___ strong

___ guilty

___ scared

___ hostile

___ enthusiastic

___ proud

___ irritable

___ alert

___ ashamed

___ inspired

___ nervous

___ determined

___ attentive

___ jittery

___ active

___ afraid

Appendix 3

Supplemental analyses for general memory trade-off performance, which was defined by '4', '5', and '6' old responses on the 1-6 confidence scale.

Examining Differences Memory Trade-offs Between Sleep And Wake Groups For Negative, Positive, And Distinctive Composite Scenes

Based on strong a priori hypotheses that sleep would enhance memory trade-offs for emotional and distinctive scenes, three separate repeated-measures ANOVAs with category (experimental category, neutral) and scene component (item, background) were conducted. Each of the experimental conditions (negative, positive, and distinctiveness) was compared to neutral. For each of these repeated-measures ANOVAs, interval (sleep, wake) was a between-subjects factor. For the negative category, there was not a significant main effect for interval $F(1, 36) = 0.67, p = 0.42, \eta_G^2 = 0.02$, but there was a significant main effect for category $F(1, 36) = 4.21, p = 0.05, \eta_G^2 = 0.05$ and for scene component $F(1, 36) = 107.61, p < 0.005, \eta_G^2 = 0.75$. There was also a significant interaction between category and component $F(1, 36) = 45.10, p < 0.005, \eta_G^2 = 0.56$, which indicates that there was an overall trade-off effect. However, there were no significant interactions between interval and category $F(1, 36) = 0.42, p = 0.52, \eta_G^2 = 0.01$, nor between interval and component $F(1, 36) = 0.68, p = 0.42, \eta_G^2 = 0.004$. In addition, there was no three-way interaction between interval, category, and component $F(1, 36) = 0.004, p = 0.95, \eta_G^2 = 0.00$ indicating that, although there is an overall trade-off for negative scenes it does not differ between sleep and wake groups (see Figure 4 in manuscript). For the positive category, there was not a significant main effect for interval $F(1, 36) = 1.025, p = 0.32, \eta_G^2 = 0.27$, but there was a significant main effect for category

F(1, 36) = 15.29, $p < 0.005$, $\eta_G^2 = 0.30$, and a significant main effect for component *F*(1, 36) = 91.42, $p < 0.005$, $\eta_G^2 = 0.73$. There was also a significant interaction between category and component *F*(1, 36) = 7.19, $p = 0.01$, $\eta_G^2 = 0.17$, which indicated that there was an overall memory trade-off effect for positive scenes. However, there were no significant interactions between interval and category *F*(1, 36) = 0.15, $p = 0.71$, $\eta_G^2 = 0.00$, nor between interval and component *F*(1, 36) = 1.08, $p = 0.31$, $\eta_G^2 = 0.01$. In addition, there was no three-way interaction between interval, category, and component *F*(1, 36) = 0.05, $p = 0.82$, $\eta_G^2 = 0.00$ indicating that, although there is an overall trade-off for positive scenes it does not differ between sleep and wake groups (see Figure 5 in manuscript). Finally, for the distinctive category, there was not a significant main effect for interval *F*(1, 36) = 1.30, $p = 0.26$, $\eta_G^2 = 0.00$, or for category *F*(1, 36) = 01.45, $p = 0.24$, $\eta_G^2 = 0.04$, but there was a significant main effect for component *F*(1, 36) = 108.62, $p < 0.005$, $\eta_G^2 = 0.75$. There was also a significant interaction between category and component *F*(1, 36) = 39.10, $p < 0.005$, $\eta_G^2 = 0.51$, which indicates that there is an overall memory trade-off effect. However, there were no significant interactions between interval and category *F*(1, 36) = 0.08, $p = 0.78$, $\eta_G^2 = 0.00$, nor between interval and component *F*(1, 36) = 0.09, $p = 0.77$, $\eta_G^2 = 0.00$. In addition, there was no three-way interaction between interval, category, and component *F*(1, 36) = 0.95, $p = 0.34$, $\eta_G^2 = 0.01$. Thus for distinctive scenes, although there is no overall difference in memory performance, when components are collapsed, there is an overall memory trade-off for distinctive scenes. However this memory trade-off does not differ between sleep and wake groups (see Figure 6 in manuscript).

Planned comparison independent t-tests further confirmed that there was no difference in corrected recognition performance between sleep and wake groups for negative items $t(36) = -0.98$, $p = 0.84$, positive items $t(36) = -0.15$, $p = 0.88$, distinctive items $t(36) = 0.76$, $p = 0.45$, and neutral items $t(36) = 0.28$, $p = 0.78$, backgrounds paired with negative items $t(36) = 0.89$, $p = 0.38$, backgrounds paired with positive items $t(36) = 1.16$, $p = 0.25$, backgrounds paired with distinctive items $t(36) = 0.57$, $p = 0.57$, and backgrounds paired with neutral objects $t(36) = 1.29$, $p = 0.21$.

Investigating Differences In The Magnitude Of The Memory Trade-off Between Sleep And Wake Groups

In order to determine whether there might be a difference in the magnitude of a memory trade-off for either emotional or distinctive scenes after a interval that included either sleep or wakefulness, repeated-measures ANOVAs were conducted using difference scores. Difference scores were calculated by subtracting the neutral corrected recognition performance for items and backgrounds from the corrected recognition performance for the items and backgrounds in the three (negative, positive, and distinctive) experimental conditions (e.g., difference score for negative items = corrected recognition for negative items – corrected recognition for neutral items). The benefit of using differences scores for these comparisons is that the difference score provides a measure of the magnitude of difference between neutral, or the baseline, and the experimental condition, which can then be compared statistically with an ANOVA. A repeated-measures ANOVA with interval (sleep, wake) as the between-subjects factor and category (negative, positive, and distinctive) and component (item, background) as within-subjects factors did not result in a significant main effect for interval $F(1, 36) =$

0.28, $p = 0.60$, $\eta_G^2 = 0.01$, but there was a main effect for category $F(2, 72) = 4.32$, $p = 0.02$, $\eta_G^2 = 0.11$ and component $F(2, 72) = 38.75$, $p < 0.005$, $\eta_G^2 = 0.52$. There was a significant interaction between category and component $F(2, 72) = 5.19$, $p = 0.01$, $\eta_G^2 = 0.12$ suggesting there was is statistical difference in the magnitude of the memory trade-offs between emotional and distinctive conditions. However there were no significant interaction between interval and category; $F(2, 72) = 0.12$, $p = 0.89$, $\eta_G^2 = 0.00$, interval and component, $F(2, 72) = 0.06$, $p = 0.81$, $\eta_G^2 = 0.00$ and no three-way interaction between interval, category, and component $F(2, 72) = 0.70$, $p = 0.50$, $\eta_G^2 = 0.02$. These suggests that there was no statistical difference in the magnitude of the memory trade-off effect between sleep and wake interval groups, which is consistent with the previous ANOVAs measuring whether there was a difference between interval conditions in the memory trade-off effect.

Planned comparison independent t-tests examining interval conditions confirmed that there was no significant difference between interval conditions for magnitude of memory differences for negative items; $t(36) = -0.53$, $p =0.60$, negative backgrounds; $t(36) = -0.43$, $p = 0.67$, positive items; $t(36) = -0.51$, $p = 0.61$, positive backgrounds; $t(36) = -0.06$, $p = 0.95$, distinctive objects; $t(36) = 0.64$, $p =0.53$, and distinctive backgrounds; $t(36) = -0.78$ $p =0.44$.

As there were overall differences, regardless of interval group, in the magnitude of memory trade-offs between emotional and distinctive conditions, paired t-tests were conducted. Paired t-tests showed that the difference score for positive backgrounds was larger than both negative; $t(37) = -3.16$, $p = 0.003$ and distinctive backgrounds; $t(37) = 3.57$, $p = 0.001$. There were no other differences between conditions for items or backgrounds. These results indicate that there are differences between the three experimental conditions for the magnitude of the item memory.

Appendix 4

Supplemental analyses for high-confidence memory trade-off performance, which was defined by ‘5’ and ‘6’ old responses on the 1-6 confidence scale.

Examining Differences In Memory Trade-offs Between Sleep And Wake Groups For Negative, Positive, And Distinctive Composite Scenes

In addition to analyses of overall recognition performance, recognition performance for high-confidence responses was also analyzed (e.g., corrected recognition calculated using hits and false alarms corresponding to “5” and “6” confidence responses). A repeated-measures ANOVA with factors of interval (sleep vs. wake) as a between-subjects factor, and factors of category (negative, positive, distinctive, neutral) and scene component (item vs. background) as within-subjects factors was conducted. There was not a significant main effect for interval $F(1, 35) = 0.53$, $p = 0.47$, $\eta_G^2 = 0.31$, but there was a significant main effect for category $F(3, 105) = 6.92$, $p < 0.005$, $\eta_G^2 = 0.16$ and component $F(1, 35) = 201.38$, $p < 0.005$, $\eta_G^2 = 0.85$. There was a significant interaction between category and component $F(3, 105) = 20.01$, $p < 0.005$, $\eta_G^2 = 0.36$ indicating that there was an overall memory trade-off. However, there was no significant interactions between interval and category $F(3, 105) = 0.25$, $p = 0.87$, $\eta_G^2 = 0.01$ and interval and component $F(1, 35) = .34$, $p = 0.56$, $\eta_G^2 = 0.00$, and no three way interaction between interval, category, and component $F(3, 105) = 1.34$, $p = 0.27$, $\eta_G^2 = 0.02$ indicating that the different components that make up a memory trade-off did not differ between sleep and wakefulness.

Due to strong a priori hypotheses that there would enhanced memory trade-offs for emotional and distinctive scenes after sleep, we conducted three separate repeated-measures ANOVAs with category (experimental category, neutral) and component (item, background), comparing each of the experimental conditions (negative, positive, and distinctiveness) to neutral. For each of these repeated-measures, interval (sleep vs. wake) was a between-subjects factor. For the negative category, there was not a significant main effect for interval $F(1, 35) = 0.29$, $p = 0.59$, $\eta_G^2 = 0.01$, but there was a significant main effect for category $F(1, 35) = 5.23$, $p = 0.03$, $\eta_G^2 = 0.13$ and for component $F(1, 35) = 161.01$, $p < 0.005$, $\eta_G^2 = 0.82$. There was also a significant interaction between category and component $F(1, 35) = 38.72$, $p < 0.005$, $\eta_G^2 = 0.52$, which indicates that there was an overall memory trade-off. However, there were no significant interactions between interval and category $F(1, 35) = 0.52$ $p = 0.48$, $\eta_G^2 = 0.01$, nor between interval and component $F(1, 35) = 0.31$, $p = 0.58$, $\eta_G^2 = 0.00$. In addition, there was no three-way interaction between interval, category, and component $F(1, 35) = 0.81$, $p = 0.37$, $\eta_G^2 = 0.02$ indicating that, although there is an overall trade-off for negative scenes it does not differ between sleep and wake groups (Figure 1S below).

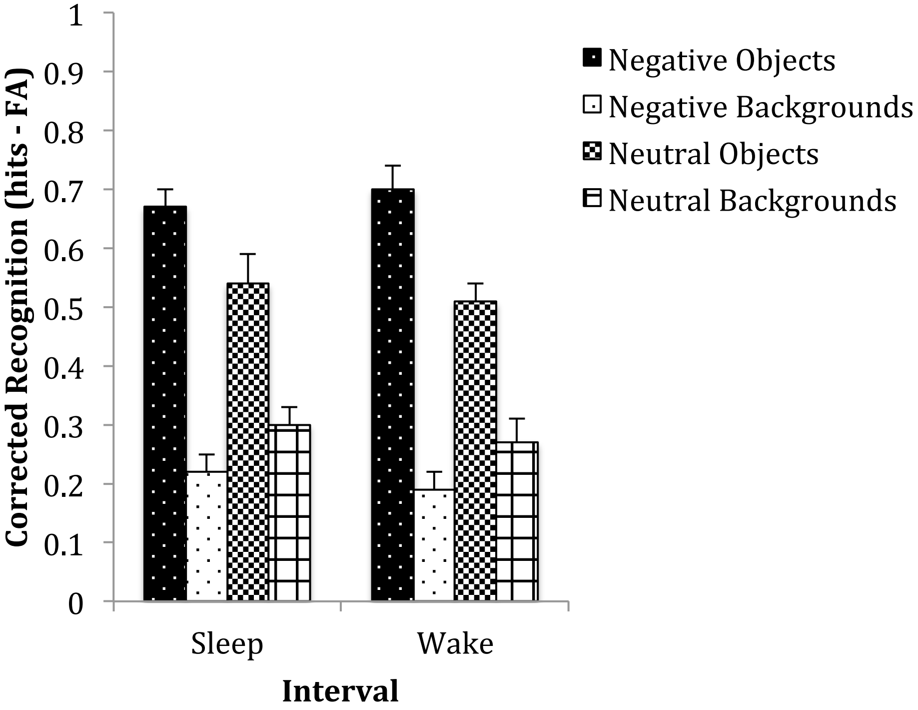

Figure 1S: Memory trade-off performance for high confidence responses for negative scenes for sleep-interval and wake-interval conditions.

For the positive category, there was not a significant main effect for interval $F(1, 35) = 0.63$, $p = 0.43$, $\eta_G^2 = 0.02$, but there was a significant main effect for category $F(1, 35) = 19.62$, $p < 0.005$, $\eta_G^2 = 0.36$, and a significant main effect for component $F(1, 35) = 89.57$, $p < 0.005$, $\eta_G^2 = 0.72$. There was also a significant interaction between category and component $F(1, 35) = 9.16$, $p = 0.01$, $\eta_G^2 = 0.20$, which indicates that there was an overall memory trade-off. However, there were no significant interactions between interval and category $F(1, 35) = 0.03$, $p = 0.86$, $\eta_G^2 = 0.00$, nor between interval and component $F(1, 35) = 0.57$, $p = 0.45$, $\eta_G^2 = 0.00$. In addition, there was no three-way interaction between interval, category, and component $F(1, 35) = 1.68$, $p = 0.20$, $\eta_G^2 = 0.04$, indicating that, although there is an overall trade-off for positive scenes it does not differ between sleep and wake groups (Figure 2S below).

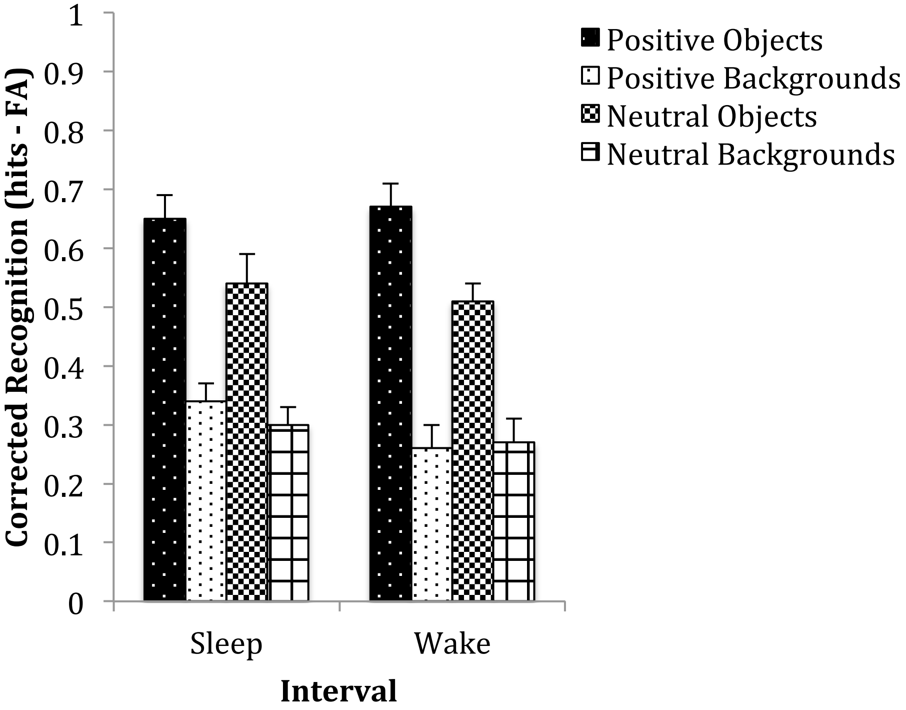

Figure 2S: Memory trade-off performance for high confidence responses for positive scenes for sleep-interval and wake-interval conditions.

Finally, for the distinctive category, there was not a significant main effect for interval $F(1, 35) = .82$, $p = 0.37$, $\eta_G^2 = 0.02$, or for category $F(1, 35) = 0.59$, $p = 0.45$, $\eta_G^2 = 0.02$, but there was a significant main effect for component $F(1, 35) = 110.82$, $p < 0.005$, $\eta_G^2 = 0.76$. There was also a significant interaction between category and component $F(1, 35) = 44.89$, $p < 0.005$, $\eta_G^2 = 0.56$. However, there were no significant interactions between interval and category $F(1, 35) = 0.01$, $p = 0.92$, $\eta_G^2 = 0.00$, nor between interval and component $F(1, 35) = 0.07$, $p = 0.80$, $\eta_G^2 = 0.00$. In addition, there was no three-way interaction between interval, category, and component $F(1, 35) = 0.16$, $p = 0.69$, $\eta_G^2 = 0.00$, which indicates that although there is no overall difference in memory performance, when components are collapsed, there is an overall memory trade-off for distinctive scenes. However the memory trade-off for distinctive scenes does not differ between sleep and wake groups (Figure 3S).

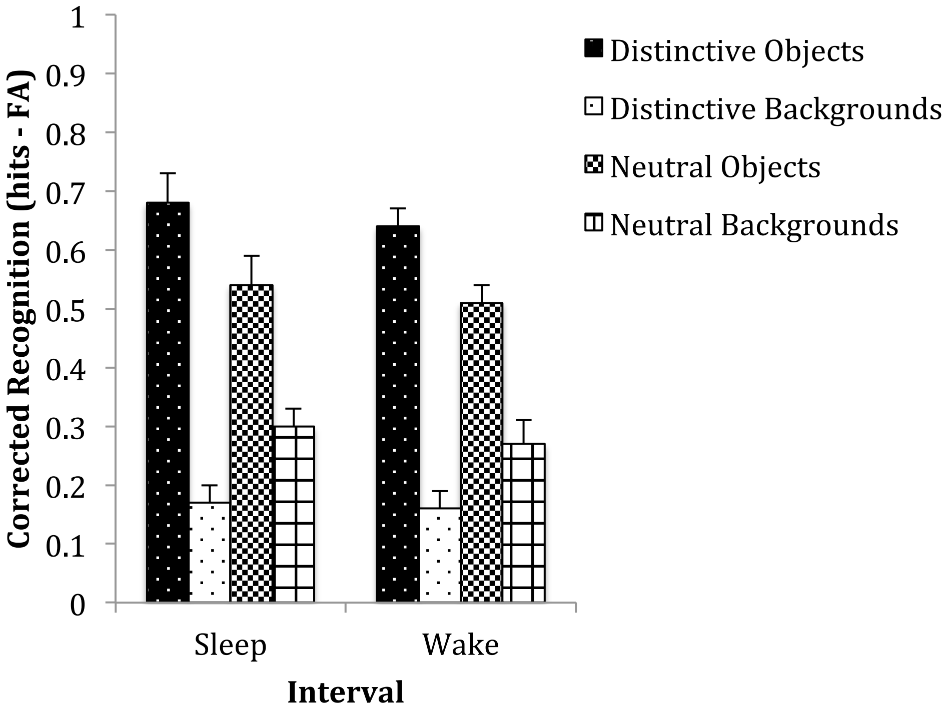

Figure 3S: Memory trade-off performance for high confidence responses for distinctive scenes for sleep-interval and wake-interval conditions.

Planned comparison independent t-tests confirmed that there was no difference in corrected recognition performance between sleep-interval and wake-interval groups for negative items $t(35) = -0.60$, $p = 0.55$, positive items $t(35) = -0.42$, $p = 0.67$, distinctive items $t(35) = 0.74$, $p = 0.46$, and neutral items $t(35) = 0.55$, $p = 0.59$, backgrounds paired with negative items $t(35) = 0.83$, $p = 0.41$, backgrounds paired with positive items $t(35) = 1.42$, $p = 0.17$, backgrounds paired with distinctive items $t(35) = 0.28$, $p = 0.78$, and backgrounds paired with neutral objects $t(35) = 0.63$, $p = 0.53$.

As there were overall differences, regardless of interval group, in the memory trade-off effect for the different categories, as evidenced by the significant interactions between category and scene component, paired t-tests were conducted. Corrected recognition for negative items was significantly higher than neutral items; $t(36) = 5.37$, $p < 0.005$, as were positive items; $t(36) = 5.26$, $p < 0.005$ and distinctive items; $t(36) = 5.73$, $p < 0.005$. Paired t-tests also confirmed that corrected recognition for backgrounds paired with negative items was significantly lower than backgrounds paired with neutral items; $t(36) = -3.00$, $p = 0.01$, as were backgrounds paired with distinctive items; $t(36) = -5.01$, $p < 0.005$. Backgrounds paired with positive items, however, were not significantly lower than backgrounds paired with neutral items; $t(36) = 0.70$, $p = 0.49$. These results suggest that memory trade-offs occur for both negatively arousing stimuli and distinctive stimuli, due to both enhanced memory for negative and distinctive items and reduced memory for negative and distinctive backgrounds. Positive emotion, on the other hand, only elicited a boost in memory for the item and did not show the accompanying decrease in memory for the backgrounds paired with positive objects, which is the hallmark of a memory trade-off. This is consistent with what was observed for general corrected recognition memory.

Investigating Differences In The Magnitude Of The Memory Trade-off Between Sleep And Wake Groups

In order to determine whether there might be a difference in the magnitude of a memory trade-off for either emotional or distinctive scenes after a interval that included either sleep or wakefulness, repeated-measures ANOVAs were conducted using difference scores. A repeated-measures ANOVA with interval (sleep, wake) as the between-subjects factor and category (negative, positive, and distinctive) and component (item, background) as within-subjects factors did not result in a significant main effect for interval $F(1, 35) = 0.28$, $p = 0.60$, $\eta_G^2 = 0.01$, but there was a main effect for category

$F(2, 70) = 5.52$, $p = 0.01$, $\eta_G^2 = 0.14$ and component $F(2, 70) = 39.88$, $p < 0.005$, $\eta_G^2 = 0.53$. There was a significant interaction between category and component $F(2, 70) = 8.36$, $p = 0.001$, $\eta_G^2 = 0.18$ suggesting there was is statistical difference in the magnitude of the memory trade-offs between emotional and distinctive conditions. However there were no significant interaction between interval and category; $F(2, 70) = 0.25$, $p = 0.78$, $\eta_G^2 = 0.01$, interval and component, $F(2, 70) = 0.54$, $p = 0.47$, $\eta_G^2 = 0.01$ and interval, category, and component $F(2, 70) = 1.85$, $p = 0.17$, $\eta_G^2 = 0.04$, suggesting that there was no statistical difference in the magnitude of memory trade-offs between sleep and wake interval groups.

Planned comparison independent t-tests examining interval conditions confirmed that there was no significant difference between interval conditions for magnitude of memory differences for negative items; $t(35) = -1.06$, $p =0.60$, negative backgrounds; $t(35) = 0.10$, $p = 0.92$, positive items; $t(35) = -1.17$, $p = 0.25$, positive backgrounds; $t(35) = -0.79$, $p = 0.44$, distinctive items; $t(35) = 0.25$, $p =0.80$, and distinctive backgrounds; $t(35) = -0.38$ $p =0.70$.

As there was an overall difference in the magnitude of memory trade-offs between emotional and distinctive scenes, paired t-tests were conducted and revealed that the difference score for positive backgrounds was larger than both negative; $t(36) = -3.47$, $p = 0.001$ and distinctive backgrounds; $t(36) = 4.88$, $p < 0.005$. There were no other differences between conditions for items or backgrounds. These results indicate that there are differences between the three experimental conditions for the magnitude of the memory trade-off effect.

The Effect of Different Sleep Stages on Memory Consolidation of Emotional and Distinctive Composite Scenes: A Napping Study

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Abstract

Sleep has been found to magnify emotional memory trade-offs, a phenomenon during which memory for salient aspects of emotional scenes is enhanced at the expense of the background, neutral information associated with the scene. It has been demonstrated that distinctive, non-emotional stimuli can elicit similar memory trade-offs, suggesting similar cognitive processes may underlie trade-offs for salient emotional and distinctive information. It is unknown whether sleep also selectively enhances memory for distinctive information. The current study aimed to investigate effects of sleep on memory trade-offs for distinctive and emotional information. Participants incidentally encoded scenes consisting of a central item (either negative, positive, neutral, or visually distinctive but emotionally neutral) against neutral scene backgrounds. After a 2-hour interval, which included a polysomnography-recorded nap or equivalent period of wakefulness, participants performed a recognition test on items and backgrounds separately. There was no enhancement in memory trade-offs for either distinctive or emotional scenes after sleep but there was a general non-significant enhancement for salient central items for all composite scenes and a significant increase in memory for neutral items after sleep. There were also non-significant correlations between Stage 2 sleep (and sleep spindle density) and memory for negative backgrounds and a significant correlation between Stage 2 sleep and positive item memory, suggesting Stage 2 sleep may mediate strengthening of information during a nap. Selective enhancement of neutral items after sleep suggest under certain circumstances sleep also preferentially consolidates neutral information and that what information is ultimately enhanced after sleep may be dependent on the situation.

Keywords: Memory trade-off, sleep-dependent consolidation, distinctiveness, emotion, nap

The effect of different sleep stages on memory consolidation of emotional and distinctive composite scenes: a napping study

Over the past decade there has been an increasing awareness amongst scientists and non-scientists that sleep can benefit cognition, and in particular memory. Understanding how sleep benefits memory paves the way to further elucidating the function of sleep, which has so far eluded scientists. Previous studies have shown that sleep can selectively enhance memory for emotionally arousing information by increasing memory trade-offs (salient aspects of emotional scenes is enhanced at the expense of the background, neutral information associated with the scene) (Payne et al., 2008). It has also previously been demonstrated that other factors, such as distinctiveness can elicit memory trade-offs (Campanella & Hamann, in preparationa, in preparationb), suggesting that emotional and distinctive information may be selectively filtered for memory enhancements through a common or overlapping mechanism. One possible way in which both types of information can be preferentially remembered is through consolidation through sleep. However, it is unclear how sleep selectively consolidates distinctive information. The goal of the present research was to address these issues by examining the relation between memory trade-offs for emotional and distinctive and different sleep stages in a memory trade-off paradigm with a polysomnography-recorded nap. As a result, memory for different components of emotional and distinctive scenes was tested and later correlate memory performance with characteristics of sleep.

Increasing evidence suggests that sleep plays a beneficial role in episodic memory processing (Diekelmann & Born, 2010; Ellenbogen et al., 2006; Stickgold, 2005, 2006). It has been demonstrated that memory for episodes is preferentially enhanced following a period of sleep directly after learning, compared to when learning is followed by an equivalent period of wakefulness, suggesting that sleep impacts slower, offline processes including memory consolidation (Diekelmann & Born, 2010; Ellenbogen et al., 2006; Stickgold, 2005; Walker & Stickgold, 2006). These beneficial effects are seen both after a full night of sleep (Backhaus, Hoeckesfeld, Born, Hohagen, & Junghanns, 2008; Gais & Born, 2004a, 2004b) and a nap (Alger et al., 2012; Lemos, Weissheimer, & Ribeiro, 2014; Masaki Nishida & Walker, 2007). In addition to benefitting memory, it has been demonstrated that sleep also protects memories from future interference (Alger et al., 2012; Ellenbogen, Hulbert, Jiang, & Stickgold, 2009; Ellenbogen et al., 2006). Moreover, evidence suggests that there is a direct relationship between improvements in memory performance and physiological correlates of sleep—rapid eye movement (REM) sleep and non-REM (NREM) sleep—suggesting sleep plays an active role in mediating memory (Ackermann & Rasch, 2014; Alger et al., 2012; Cairney et al., 2014; Diekelmann et al., 2012; Gais & Born, 2004b; Peigneux et al., 2004; Wagner et al., 2001). NREM stages of sleep, and more specifically slow wave sleep (SWS), have been shown to benefit declarative memory. Gais et al, (2004) demonstrated that properties of SWS, specifically low levels of acetylcholine, were ideal for consolidation of verbal memory.

A prominent theory suggests that sleep consolidates memories by reactivating recently encoded memories during sleep (Born & Wilhelm, 2012). The effect is perhaps more specific to NREM stages of sleep. Extracellular in vivo studies investigating SWS physiology have demonstrated that neocortical neurons will spontaneously reactivate during SWS, which in turn may strengthen memory traces (Steriade & Timofeev, 2003).

Animal studies have demonstrated that recently acquired hippocampus-dependent memories are ‘replayed’ (same patterns of neural firing in hippocampus observed during learning are repeated) during SWS, thus implicating offline consolidation processes (O’Neill et al., 2006; Wilson & McNaughton, 1994). Similar evidence has been reported in humans using a virtual maze task and positron emission tomography (PET) scanning (Peigneux et al., 2004). Hippocampal activity that was associated with initial learning during waking hours later re-emerged during SWS. More significantly, the amount of SWS reactivation in the hippocampus was proportional to the amount of improvement in the maze task the next day, thus suggesting that this reactivation is associated with offline memory consolidation. Studies have also demonstrated that re-presenting cues, either odor (Rasch et al., 2007) or sound (Rudoy et al., 2009) cues, during SWS significantly improved memory performance compared to a control condition where no cue was re-presented suggesting sleep may actively reprocess memories during SWS. Recently, however, it has been demonstrated using shorter delays (40 min and 90 min naps) that reprocessing of memories during sleep may also be dependent on time spent sleeping, in addition to time spent in SWS (Diekelmann et al., 2012).

Increasingly it has been demonstrated that sleep does not globally consolidate all information that is learned, but instead may selectively consolidate highly salient information for long-term memory. Studies in animals demonstrate that rewarded information is preferentially reactivated in the hippocampus and ventral striatum during sleep (Lansink et al., 2008, 2009). Studies in humans support these findings as it has been demonstrated that rewarded information is preferentially reactivated during sleep in humans (Oudiette & Paller, 2013). Using a cue-dependent recall task, Oudiette et al.

instructed participants to remember the location of everyday objects presented on a screen. Objects were assigned a value that represented a future payoff (either low or high value) for successful subsequent memory retrieval, thereby manipulating the object's salience, and subsequently reactivated during targeted reactivation during sleep and wake. Interestingly, only low-value items were selectively enhanced by sleep, whereas memory for high-value items did not differ by delay period (i.e., wakefulness or sleep), suggesting that high reward information may not always be exclusively consolidated during sleep. In addition, there may be additional factors, not exclusively related to reward, that mediate what information is selectively consolidated during sleep.

Information that is not externally rewarded can also been selectively consolidated during sleep. For example, it has been demonstrated that the mere expectancy that information would be used in a future memory test determined whether sleep could significantly benefit subsequent memory performance. Additionally, the memory enhancement in the group expecting a memory test was also strongly correlated with features of SWS (Wilhelm et al., 2011). Several studies using a directed forgetting memory paradigm corroborate such findings by demonstrating that sleep selectively consolidates information that participants were cued to remember (Rauchs et al., 2011; Saletin et al., 2011). Moreover, Saletin et al, (2011) discovered that the selective enhancement for cued information was correlated with fast spindle activity, which is a hallmark of Stage 2 sleep though also present in SWS (Mölle et al., 2002). In sum, reactivation during NREM sleep stages—specifically SWS but also perhaps Stage 2 sleep—may selectively target memories that motivationally important to remember.

Despite the possible relationship between memory performance and stage 2 sleep alluded to by Saletin et al, 2011, there is a paucity of studies investigating the effects of stage 2 sleep on memory consolidation (for review, see Ruch et al., 2012). This is likely due to a previous lack of understanding of what sleep spindles represented. Sleep spindles are transient high-frequency electroencephalographic oscillations (12-16 Hz) that last for at least 0.5 sec (Rechtschaffen & Kales, 1968). Temporally, sleep spindles are connected to hippocampal ripples (Marshall & Born, 2007) and are said to be when neurons replay previous waking activity (Buzsaki et al., 1992; Buzsaki, 1998). It is possible that sleep spindles in humans reflect the same underlying process identified by replay in animals. The potential relationship between spindle activity, which are found in NREM sleep stages, and memory consolidation highlight the importance in determining the role that different stages of NREM sleep have on mediating memory consolidation.

A hallmark of the previously mentioned studies investigating the effects of sleep on selectively consolidating memory is that saliency was externally motivated by the experimenter, either through external rewards or by informing participants of the importance of the information. Questions still remain about the mechanisms that mediate selective consolidation of information that is inherently salient to an individual, without experimenter interference, which may better reflect how information is consolidated naturally. In order to address such questions, experimenters look to stimuli that are naturally salient or relevant, such as emotional information. It has been well established that emotional information is better remembered than neutral information (Hamann, 2001; LaBar & Cabeza, 2006; LeDoux, 1993; McGaugh, 2004). There are evolutionary benefits to remembering emotional information. For example it is evolutionarily advantageous to remember threats so as to avoid them in the future. Evidence suggests that sleep may preferentially consolidate emotional information (Hu et al., 2006; Wagner et al., 2001). Consolidation of emotional information during sleep, however, is not uniform. Instead, selective elements of an emotional scene, specifically the thematically central and/or highly salient elements, are preferentially consolidated compared to other elements or the background (Payne et al., 2008; Payne & Kensinger, 2011a). Moreover, increasing evidence suggests it is REM sleep, as opposed to NREM sleep stages, that mediate consolidation of emotional information (Ackermann & Rasch, 2014; Groch et al., 2013; Nishida et al., 2009; van der Helm et al., 2011; Wagner et al., 2001). In particular, physiological characteristics of REM sleep, specifically high levels of cortisol and increases in hippocampal and amygdala activation, may provide the ideal neurobiological environment for consolidation of emotional information (Born & Wagner, 2004; Payne & Kensinger, 2010; Payne & Nadel, 2004; Walker & van Der Helm, 2009).

Conversely, it has been demonstrated that NREM sleep, and more specifically SWS sleep, may also play a role in selective emotional memory consolidation. A recent nap study demonstrated that sleep preserved emotional (negative) aspects of complex experiences at the expense of neutral aspects, but that the enhancement in memory for the emotional aspects was correlated with time spent in SWS, thus implicating SWS in consolidation of negatively salient information (Payne & Kensinger, 2011b). More recently, a fMRI study investigating the roles of SWS and REM sleep (over the course of an entire night) on memory consolidation for emotional images demonstrated that emotionally charged memories might first be selectively reorganized away from the hippocampus during SWS and then targeted for emotional processing during subsequent REM sleep (Cairney et al., 2014), suggesting a complementary role of both NREM and REM sleep stages in emotional memory consolidation.

The conflicting findings presented above suggest that conditions underlying preferential consolidation of emotional memories over sleep require further examination. Most of the previous studies measured consolidation over the course of a full night's sleep, which includes both periods of NREM and REM sleep. Although most implicated REM sleep as being critical for strengthening emotional memories, they cannot unequivocally exclude the influence of NREM sleep stages. Moreover, nap studies, during which little REM occurs also demonstrate a preferential emotional memory benefit suggesting that REM sleep may not always been necessary for emotional memory processing (Payne & Kensinger, 2011b). Instead, it is possible that emotional memories are somehow 'tagged' as salient during encoding and that this tag is what determines what information is then consolidated during sleep. Cortisol levels during learning have been implicated as one possible factor that could facilitate this tagging of information (Bennion et al., 2013). However other factors could also help tag information for selectively memory consolidation.

It is important to note that the previous studies primarily defined emotion in terms of the dimension of emotional arousal (i.e., calm or relaxed to excited or agitated). Emotion, however, can also be defined by other factors and it is possible that these other factors may interact with sleep to mediate memory consolidation. In addition to being defined by its associated arousal, emotion is also defined in terms of the dimensional scale of valence (highly positive to highly negative) (Lang et al., 1993; Russell, 1980).

Furthermore, some studies suggest that there might differences in memory performance for negative and positive stimuli (Kensinger & Schacter, 2006; Kensinger, 2004; Ochsner, 2000); and more specifically, that negative stimuli are more vividly remembered. Other studies, however, suggest that there is no difference in memory performance for positive and negative stimuli (Cahill & McGaugh, 1998) and the effect of emotion on consolidation is primarily due to arousal. Thus, as it is unclear valence differentially affects cognitive processing, it is important to determine whether there is an interaction between valence and sleep in memory consolidation.

Emotion can also be defined by its non-affective features, such as how distinctive a stimulus is and how much attention it attracts. For example, emotional stimuli are often considered to be unexpected, perceptually unusual, and out of place within the current context, and thus also considered to be distinctive (Ochsner, 2000). Moreover, it has been demonstrated that both emotion (Buchanan & Adolphs, 2002; Christianson & Fällman, 1990; Hamann, 2001; Talmi et al., 2007; Thomas & Diener, 1990) and distinctiveness (Blackford et al., 2010; Itti & Baldi, 2009; Mitchell et al., 1998; Pickel, 1998; Ranganath & Rainer, 2003) preferentially attract attentional and cognitive processing resources at encoding, which ultimate results in better subsequent memory. Thus, it is possible that distinctiveness, like affective features such as arousal, may also preferentially tag information to be consolidated during sleep through a common mechanism. However, what that mechanism might be is currently unclear.

The goal of the current study was to elucidate how distinctiveness and affective factors of emotion tag information for selective memory consolidation by determining the relationship between different sleep stages and memory performance for distinctive and emotional information. Using a similar paradigm to the overnight study presented in the previous chapter, we presented participants with pictures of scenes consisting of a target item (either negative, positive, neutral, or distinctive but emotionally neutral) superimposed over neutral indoor and outdoor background scenes. After a 2 hour interval, during which participants had a polysomnography-recorded nap or experienced an equivalent period of wakefulness in the lab, participants received an unannounced recognition test where they were tested on the central items and backgrounds separately in order to assess memory for each of these two elements. A nap was used as opposed to an overnight paradigm in order to eliminate any possible diurnal effects on cognition. Polysomnography was used to measure time spent in different sleep stages, which was then measured in relation to subsequent memory performance. It is possible that the initial strengthening of newly learned salient information, or more specifically whatever was strongly encoded during initial learning, could occur during SWS sleep, whereas REM sleep could selectively preserve emotional reactivity, leading to an additional boost for those emotionally-charged memory traces. Alternatively, REM sleep could also serve to additionally boost distinctive information to the same degree as emotional information, suggesting a common mechanism at work. In addition it is currently unclear what the role of stage 2 sleep, the other prescient NREM sleep stage, is in this mechanism.

Describing the relation between sleep stages and selective memory performance for emotional and distinctive scenes serves two purposes. First, it will increase understanding about what factors may selectively filter information for memory consolidation during sleep. Secondly, it could begin to illuminate how sleep consolidates different components of emotion. Sleep could consolidate different components of emotion through a common process (reflected by correlations between memory for emotional and distinctive factors and the same sleep stage). Alternatively, different components of emotion could differentially interact with sleep for an additive overall behavioral effect (e.g., increase in memory for distinctive factors correlating with SWS, whereas increase in memory for emotional factors correlating with REM sleep).

Methods

Participants

Thirty-six students from Emory University participated for payment or class credit. Six participants were excluded from the final analysis for various reasons: four participants were excluded for poor data[4], one participant was excluded for suspecting a memory test, and one participant was excluded for failing to fall asleep during the nap period. The final data set included 30 students from Emory University (mean age= 20.53 years, *SEM*= 0.47). None of the participants had participated in the overnight study described in the previous chapter. Participants were randomly assigned to one of two conditions, either a napping condition (N= 15, 11 females) or a wake condition (N= 15, 10 females). All participants were native English speakers with normal to corrected-to-normal vision. No participant reported a history of sleep disorders or was taking medications that might affect their sleep cycle. Participants were also instructed not to consume alcohol or caffeine for the duration of the study. Furthermore, participants were asked to keep a sleep log during the week prior to the first session. On average participants slept an average of 7.58 hours per night (*SEM*= 0.19). There were no systematic differences in average sleep per night for the nap and wake groups (*M*= 7.38,

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[4] Corrected recognition performance for neutral backgrounds was less than zero

SEM= 0.35 vs. *M*= 7.78, *SEM*= 0.16, *p*= 0.29). In addition, Epworth Sleepiness Scale scores were collected to measure daytime sleepiness and no systematic differences were observed between nap and wake groups (*M*= 10.07, *SEM*= 1.00 vs. *M*= 9.36, *SEM*= 0.76, *p*= 0.57). Complete demographics information on all participants is included in Table 1. Written informed consent was obtained from all participants and the study was approved by the Emory University Institutional Review Board.

Materials

Composite scenes

Visual composite scenes were used in this study the effect of a nap on memory trade-offs. The visual stimulus set used to test the effect of sleep on memory trade-offs was composed of 240 items (60 negative, 60 positive, 60 visually distinctive but emotionally neutral, and 60 neutral items) and 240 neutral backgrounds. Negative, positive, and neutral items were taken from those used in prior studies (Kensinger, Garoff-Eaton, & Schacter, 2007a; Waring & Kensinger, 2009). In order to create distinctive but emotionally neutral items, neutral items (e.g., a television) were modified through Photoshop (e.g., color overlay and pattern fill). Additional distinctive items, primarily chimeric animals and digitally manipulated items (e.g., a briefcase made of straw), which were rated by an additional group of participants as emotionally neutral were obtained from various internet photo-sharing sites.

Subjective emotional arousal and distinctiveness ratings for all the items were collected from all participants using a 1-5 Likert scale (1= low arousal to 5= high arousal). Emotional arousal ratings differed significantly between emotional, distinctive, and neutral item categories, distinctive and neutral item categories, and emotional and neutral item categories (see Table 2 for breakdown of arousal ratings). Subjective distinctiveness ratings for all items were also collected from all participants using a 1-5 Likert scale (1= not visually distinctive, typical to 5 = very visually distinctive, atypical). Distinctiveness ratings differed significantly between emotional, distinctive and neutral item categories, except between positive and neutral items (see Table 2 for breakdown of distinctiveness ratings).

Backgrounds consisted of neutral indoor and outdoor scenes from the International Affective Picture System (IAPS; Lang, Bradley, & Cuthbert, 2008) along with some additional neutral images taken from public domain photo-sharing internet sites. All backgrounds were formatted to a size of 1000 x 750 pixels.

Composite scenes were created by pairing items from each stimulus category with neutral backgrounds. Specifically, negative (e.g., a spiked weapon), positive (e.g., treasure chest), distinctive but emotionally non-arousing (e.g., chimeric animal that was part kangaroo, part lemur), and neutral items (e.g., a pair of boots) were individually paired with neutral backgrounds (e.g., a desert scene). Composite scenes were matched for item size, item location, visual complexity, and the semantic congruency of item and background scene.

The stimulus category of items combined with each background was counterbalanced across participants (see Figure 1 for example) to control for systematic stimulus effects of items and backgrounds. The resulting encoding lists contained of 160 composite scenes consisting of an item (40 negative, 40 positive, 40 distinctive, and 40 neutral) against a neutral background. The order of presentation for composite scenes at encoding was also counterbalanced across participants to control for order and carryover effects. Each encoding list was therefore further broken down into four lists: each containing 10 composite scenes from each category (i.e., 10 negative composite scenes, 10 positive composite scenes, 10 distinctive composite scenes, and 10 neutral composite scenes).

Subjective alertness and sleepiness questionnaires

Two questionnaires were administered to assess subjective alertness (Stanford Sleepness Scale; Hoddes et al., 1972) and daytime sleepiness (Epworth Sleepiness Scale; Johns, 1991) (see Appendix 1 for more detailed description).

Sleep measurements

In order to assess the role of sleep stage on memory consolidation for the composite scenes, polysomnography (PSG) was recorded in the participants in the NAP group. The PSG montage included EOG (right and left ocular canthus), two chin (EMG), and four cortical EEG leads (F3-A2, O1-A2, C3-A2, C4-A1). Data was obtained and analyzed according to the specifications provided in the revised AASM manual (Iber et al, 2007).

Procedure

Overview of Paradigm

Participants were randomly assigned to either the napping or wake group. All participants reported to the sleep laboratory around 1 PM – 2PM in the afternoon. Application of electrodes for PSG, for both napping and wake groups, took approximately 25 -30 min. After the initial encoding period, participants in the napping group were given a two-hour opportunity in which to nap in a sound attenuated bedroom. Sleep was monitored according to standard criteria (Iber et al, 2007) throughout the nap interval. After 2 hours, participants were woken up and electrodes were removed. Ten minutes later, when participants were fully awake, they were given a recognition test. In the wake condition, participants spent the two-hour interval between encoding and the recognition test watching television. PSG data was collected for participants in the wake condition to ensure that they did not sleep during the interval (see Figure 3, for overall paradigm). After the recognition test all participants rated the items they had seen for arousal and distinctiveness.

Measure of alertness

Before beginning the encoding and recognition sessions, participants were asked to rate their subjective feelings of alertness using the SSS.

Memory trade-off task

Encoding task: Participants were told that they would be viewing photographs of scenes and were instructed to indicate whether they would approach or avoid each scene by responding with one of three keys (1= move extremely close, 2= stay in same location, and 3= move extremely far), pressing a corresponding key on the computer keyboard. All participants practiced the rating task before the actual experiment, using a separate set of stimuli. The purpose of the approach/avoidance task was to ensure that participants were attending to the composite scene during the encoding phase.

Each encoding trial began with a fixation cross presented for a duration of 1 second, followed by the presentation of a composite scene for 3 seconds. Next, a response screen appeared for 6 seconds, during which participants were instructed to make their approachability keyboard rating response (see Figure 3, for a representative encoding trial). Participants were instructed to view the scene while it was on the screen and to wait until the response screen was presented to make their response. All participants were able respond within the time allotted. Task instructions emphasized making an accurate rather than a rapid response, and the response screen was always presented for the full 6 seconds, regardless of response reaction time. Stimulus sets were counterbalanced across runs across participants.

Recognition task: After a 2-hour interval that included either a period of wakefulness or sleep, participants were given an unannounced recognition memory test. The recognition test was not mentioned during the encoding session, to minimize potential selective rehearsal effects. Participants were told that after the delay they would be rating pictures. At test, studied items and backgrounds were presented separately and were intermixed together with new item and backgrounds. Forty old (i.e., previously presented) items and 40 old backgrounds from each of the four stimulus categories (a total of 160 old items and 160 old backgrounds) were presented intermixed with 20 new items (i.e., not previously presented) and 20 new backgrounds from each category (a total of 80 new items and 80 new backgrounds). The size and orientation of each old item and background was identical to its size and orientation during the encoding session. Participants were instructed to view each item or background and to make a recognition memory judgment using a 1-6 confidence scale (1= definitely new, 2= probably new, 3= maybe new, 4= maybe old, 5= probably old, 6= definitely old). Each item or background was presented for 3 seconds, followed by a recognition response screen. Participants were allowed an unlimited amount of time to make a response (see Figure 3, for representative retrieval trials). Participants completed a short practice recognition test (using a separate set of items) before the actual recognition test to ensure that participants fully understood the task and the response scale.

Subjective emotional ratings

Participants were asked to provide subjective ratings of emotional arousal and distinctiveness for all the items they had previously seen. Participants were instructed to rate how strong an emotional reaction they had to the object using a Likert scale of 1 (low) to 5 (high). For low arousal ratings, words like calm, relaxed, bored, or sleepy were described the endpoint whereas words like excited, nervous, or wide-awake were used to describe the high arousal endpoint. Participants were then instructed to rate how visually distinctive they found each object using a Likert scale of 1 (not distinctive) to 4 (very distinctive). Participants rated the pictures they had seen in the original encoding session.

Data Analysis

Defining memory trade-offs

The memory trade-off effect has been defined as the enhancement of memory for emotional items combined with a corresponding decrease in memory for simultaneously presented background stimuli, relative to the corresponding measures for neutral items (Kensinger, Garoff-Eaton, & Schacter, 2007a). The memory trade-off effect for positive, negative, and distinctive items was assessed by comparing corrected recognition memory performance (the proportion of hits minus the proportion of false alarms) for each of these conditions to corrected recognition memory performance in the neutral item condition. The trade-off effect for background scenes was assessed in a similar way, by comparing corrected recognition memory performance between the background scenes that had been paired with items during encoding in each corresponding condition (positive, negative, or distinctive items) and the corresponding memory measure for the backgrounds that had been paired with neutral items during encoding.

To assess recognition memory performance, the proportion of recognition hits was calculated on the basis of correctly recognized items or backgrounds that received recognition confidence responses of ‘4’, ‘5’, and ‘6’, whereas the proportion of false alarms was based on the proportion of new items or backgrounds that received recognition confidence responses of ‘4’, ‘5’, and ‘6’. In an additional analysis; high-confidence recognition responses were analyzed separately. In order to calculate high confidence memory, correct confidence responses of ‘5’ and ‘6’ were coded as ‘hits’ and incorrect confidence responses of ‘5’ and ‘6’ were coded as ‘false alarms’.

Effects of sleep and sleep stage on memory trade-offs

Sleep data was scored in accordance with the specifications provided in the revised AASM manual (Iber et al, 2007). The effect of sleep on memory trade-offs for negative, positive, distinctive, and neutral composite scenes was evaluated with repeated measures analyses of variance (ANOVAs) with category (negative, positive, distinctiveness, and neutral) and component (item and background) as within-subject factors and interval (nap and wake) as a between subjects factor. Then, three separate repeated measures ANOVAs were calculate comparing each experimental category to neutral. Effect size was assessed as general eta squared (η_G^2). Interaction effects were further evaluated with planned comparison t-tests.

In order to determine whether there were differences in the magnitude of the memory trade-offs observed between the sleep and wake groups for emotional conditions and distinctiveness, repeated-measures ANOVAs were conducted using difference scores. Difference scores were calculated by subtracting the neutral corrected recognition performance for items and backgrounds from the corrected recognition performance for the items and backgrounds in the three experimental conditions (e.g., difference score for negative items = corrected recognition for negative items – corrected recognition for neutral items). Effect size was assessed as general eta squared (η_G^2). Interaction effects were further evaluated with planned comparison t-tests.

In order to measure the association between sleep and memory performance Pearson correlations were calculated between the total time of sleep, time in stage 2 sleep, and time in slow wave sleep, and memory performance. Correlations were also performed measuring the relationship between memory performance and specific components of sleep (sleep spindles in stage 2 sleep and SWS and delta density in SWS). Supplemental correlations were also performed on a subset of participants who achieved REM sleep measuring the relation between in time REM sleep, REM latency, and memory performance.

<u>*Sleep spindle analyses:*</u> Sleep spindles were visually identified in all epochs scored as Stage 2 for the entire nap period. Spindles were visually detected using the central electrodes (C3 and C4), which were referenced to contralateral mastoids (Schabus et al., 2004). All spindles included in the final analyses were within the 12-16 Hz frequency band, exceeded 0.5 sec, and demonstrated the typical spindle morphology with a maximum amplitude that exceeded 10μV as described by (Rechtschaffen & Kales, 1968). The current methodology was not sensitive to detect the difference between fast and slow spindles and so for the following calculations, fast and slow spindles were

collapsed into one group. Spindles were counted by two independent raters and then averaged between raters. Single density was calculated using a ratio of the number of sleep spindles counted in Stage 2 sleep to the number of minutes in Stage 2 sleep as described by (Fogel & Smith, 2006).

Subjective arousal and mood ratings interval groups

In order to measure any differences in alertness between the encoding and recognition sessions, or lack thereof, paired t t-tests were performed on subjective ratings of alertness (as measured by SSS).

Results

An alpha of less than 0.05 was set a priori for all statistical analyses. Due to the relatively small sample size, P values between 0.05 and 0.10 and will be interpreted tentatively.

Subjective Alertness Between Nap and Wake Group

In order to assess whether baseline alertness was not responsible for any observed differences in memory performance between the nap-interval and wake-interval groups we measured subjective alertness using the Stanford Sleepiness Scale and found no significant differences between groups (M= 2.57, SEM= 0.23 vs. M= 3.10, SEM= 0.24, p= 0.17).

Sleep vs. Wake Memory Trade-Off Comparisons

Full descriptions of hits (correct ‘old’ responses), false alarms (incorrect ‘old’ responses), and corrected recognition performance for all items and backgrounds for nap and wake groups are listed in Table 3.

Analyzing differences in memory performance between nap and wake groups

Memory trade-off effects: To assess whether memory trade-offs were stronger after a nap for emotional and distinctive scenes, relative to neutral scenes, a repeated-measures ANOVA with factors of interval (nap vs. wake) as a between-subjects factor, and factors of category (negative, positive, distinctive, neutral) and scene component (item vs. background) as within-subjects factors was conducted. There was no significant main effect for interval group $F(1, 28) = 1.76, p = 0.195, \eta_G^2 = 0.06$ and no significant main effect for category $F(3, 84) = 0.99, p = 0.40, \eta_G^2 = 0.03$, but there was a significant main effect of scene component $F(1, 28) = 66.16, p < 0.005, \eta_G^2 = 0.68$. There was a significant interaction between category and scene component $F(3, 84) = 7.23, p < 0.005, \eta_G^2 = 0.20$ indicating that there was an overall memory trade-off, and a significant interaction between interval group and category; $F(3, 84) = 2.70, p = 0.05, \eta_G^2 = 0.09$ indicating that there were overall differences in memory performance between categories that differed between nap and wake interval groups. However, there was no significant interaction between interval group and scene component $F(1, 28) = 2.43, p = 0.13, \eta_G^2 = 0.03$, and no three way interaction between interval group, category, and scene component $F(3, 84) = .52, p = 0.64, \eta_G^2 = 0.01$ indicating that although there were overall memory differences between scene categories between nap and wake groups, there was no difference in the memory trade-off effect between nap and wake interval groups (see Figures 4, 5, and 6 for group comparisons for negative, positive, and distinctive scenes respectively).

Planned comparison paired t-tests were conducted and revealed that corrected recognition for negative items was significantly higher than neutral items; *t*(29) = 4.69, $p < 0.005$, as were positive items; *t*(29) = 3.55, $p < 0.005$ and distinctive items; *t*(29) = 2.90, $p = 0.01$. Paired t-tests also revealed that corrected recognition for backgrounds paired with negative items was significantly lower than backgrounds paired with neutral items; *t*(29) = -2.28, $p = 0.03$, as were backgrounds paired with positive items; *t*(29) = -2.05, $p = 0.05$ and backgrounds paired with distinctive items; *t*(29) = -2.97, $p = 0.01$ (Table 3). These results suggest that overall memory trade-offs occurred, regardless of post-encoding sleep, for negative, positive, and distinctive scenes due to both enhanced memory for items and reduced memory for backgrounds in all three categories, which is a hallmark of a memory trade-off.

Based on the hypothesis that sleep would increase memory trade-offs for distinctive and emotional scenes, we examined the effect of sleep on memory trade-offs for emotional and distinctive scenes in three separate repeated-measures ANOVAs with category (emotional or distinctive category, neutral) and component (item, background). For each of these repeated-measures ANOVAs, interval (nap vs. wake) was a between-subjects factor. As with the omnibus repeated-measures ANOVA, there were overall memory trade-offs for negative, positive, and distinctive scenes, which did not differ between sleep and wake groups. One difference between the two analyses, however, was that there was a significant main effect for interval group; $F(1, 28) = 4.36$, $p = 0.05$, $\eta_G^2 = 0.13$ for negative scenes, suggesting there was an overall memory difference in the negative condition between nap and wake groups. Full descriptions of these analyses can be found in Appendix 2.

Differences in magnitude of memory trade-off effects: As there were no differences in memory trade-offs between sleep and wake groups, it was unlikely that there would be differences in the magnitude of a memory trade-off for either emotional or distinctive scenes after an interval that included either sleep or wakefulness. As a result, analyses investigating possible differences in magnitude of memory trade-offs between sleep and wake group will not be discussed here. For reference, a description of such analyses are described in Appendix 2, which confirm that there were no differences in the magnitude of memory trade-off effects between nap and wake groups.

Other memory differences between interval groups: Due to the significant interaction between interval group and category in the omnibus ANOVA, which suggested that there were overall memory differences between nap and wake group for the different categories, repeated measures ANOVAs were conducted on items and backgrounds separately to further elucidate where the difference might be. In order to investigate the effect of a nap on memory for items in all categories a repeated measures ANOVA was conducted with interval group (nap vs. wake) as a between subjects factor and category (negative, positive, distinctive, and neutral) as a within subjects factor. The main effect for interval group was marginally significant $F(1, 28) = 3.83$, $p = 0.06$, $\eta_G^2 = 0.12$, and there was a significant main effect for category $F(3, 84) = 6.45$, $p = 0.001$, $\eta_G^2 = 0.18$. There was, however, no interaction between interval group and category $F(3, 84) = 0.89$, $p = 0.45$, $\eta_G^2 = 0.03$ indicating that although was an overall difference in memory for items between nap and wake groups and there was an overall difference in memory for items between categories, the memory differences between categories did not differ between interval groups (Figure 7A). Planned comparison independent t-tests demonstrated corrected recognition for items was higher for neutral items; $t(28) = 2.41$, p

= 0.02 in the nap group. Additionally, corrected recognition for negative items was marginally higher in the nap group; $t(28) = 1.84$, $p = 0.08$, which was consistent with the main effect observed earlier for interval group for the ANOVA comparing negative scenes to neutral scenes. There were no differences between nap and wake interval groups for positive items; $t(28) = 1.58$, $p = 0.13$ or distinctive items; $t(28) = 1.24$, $p = 0.23$.

A repeated measures ANOVA was also conducted with the backgrounds with interval group (nap, interval) as a between subjects factor and category (negative, positive, distinctive, and neutral) as a within subjects factor. There was no main effect for interval group $F(1, 28) = 0.03$, $p = 0.86$, $\eta_G^2 = 0.00$, but there was a significant main effect for category $F(3, 84) = 3.19$, $p = 0.03$, $\eta_G^2 = 0.10$. There was no interaction between interval group and category $F(3, 84) = 1.87$, $p = 0.14$, $\eta_G^2 = 0.06$ indicating that there were differences in memory for backgrounds between categories but there were no differences between nap and wake interval groups (Figure 7B). Planned comparison independent t-tests indicated there were no significant differences between nap and wake interval group in memory for backgrounds paired with negative items $t(22.77) = 0.44$, $p = 0.66$, backgrounds paired with positive items $t(28) = -0.34$, $p = 0.74$, backgrounds paired with distinctive items $t(28) = -1.26$, $p = 0.22$, and backgrounds paired with neutral objects $t(28) = 0.65$, $p = 0.52$.

Analyzing differences in memory trade-offs for high confidence responses between nap and wake groups

In addition to analyses of overall recognition performance, recognition performance for high-confidence responses was also analyzed (e.g., corrected recognition calculated using hits and false alarms corresponding to "5" and "6" confidence responses). This was in order to investigate whether there were differences in memory trade-off performance between groups based on how confident participants were during recognition, which may reflect recollection-type responses. However, high-confidence analyses showed almost an identical pattern as was described for general recognition performance above and will not be further discussed here. Descriptions of analyses can be found in Appendix 3. Memory performance for items and backgrounds for high-confidence responses is listed in Table 4.

Correlation Between Memory Performance And Sleep Measures

The primary interest of the current study related to the influence of sleep and different components of sleep on memory consolidation processes. Pearson correlations were conducted to measure the relation between memory performance for item and backgrounds in each of the experimental categories (negative, positive, distinctive, and neutral) and sleep measures (total time asleep, Stage 2 sleep, Stage 3 sleep, and REM). A breakdown of sleep stages during the nap can be found in Table 5. Supplemental correlations were also conducted examining the relation between memory performance and spindle density.

Correlations with time spent asleep

Pearson correlations measuring the relation between the amount of time participants in the nap group spend sleeping and subsequent memory performance showed a significant strong positive relation between the amount of time spent sleeping and memory for distinctive items $r(15) = 0.61$, $p=0.02$ and a strong positive relation between time spent sleeping and memory positive items that marginally significant $r(15)$

= 0.50, *p*=0.06 (see Table 6 for all correlations between sleep duration and memory performance).

Correlations between memory performance and time spent in slow wave sleep

Because previous research which suggests that SWS benefits declarative memory (Alger et al., 2012; Gais & Born, 2004b), and also may influence memory selectivity (Wilhelm et al., 2011), Pearson correlations were calculated to assess the relation between time spent in SWS and subsequent memory performance for all categories and components. Five of the fifteen participants in the nap group were excluded from the analysis, as they did not reach slow wave sleep during the nap period. There were no significant relations between time in SWS and memory for the different categories or scene components (see, Table 6 for all correlations between SWS and memory measures).

Correlations between memory performance and time spent in rapid eye movement sleep

Because previous research suggests that REM sleep may mediate emotional processing and benefit emotional memory (Nishida et al., 2009; Wagner et al., 2001), Pearson correlations were calculated to investigate relations between time spent in REM sleep and memory performance for all categories (negative, positive, distinctive, and neutral) and scene components (items and backgrounds). Analyses were conducted on twelve of the fifteen participants, because three of the participants in the nap group did not reach REM sleep during the allotted nap period. There were no significant relations between time in REM sleep and memory for the different categories or scene components.

Correlations between memory performance and time spent in Stage 2 sleep

Because of previous research suggesting that Stage 2 sleep and specific components of Stage 2 sleep (including sleep spindles) play a beneficial role in declarative memory (Fogel & Smith, 2006; Saletin, Goldstein, & Walker, 2011), Pearson correlations were calculated to measure the relation between time in Stage 2 sleep and memory performance for items and backgrounds in the different scene categories (negative, positive, distinctive, neutral). There was a strong positive relation between time spent in Stage 2 sleep and memory for positive items $r(15) = 0.56$, $p=0.03$ and positive relation for memory for negative backgrounds, which was marginally significant $r(15) = 0.45$, $p=0.09$ (see Table 6 for all correlations between Stage 2 sleep and memory performance).

Correlation between memory performance and spindle density

Previous studies suggest that sleep spindles, which are a signature of Stage 2 sleep, may represent information transfer between the hippocampus and neocortex (Schabus et al., 2004)—a hallmark of systems memory consolidation. As a result, in addition to measuring the relation between time spent in stage 2 sleep and subsequent memory performance, Pearson correlations were also calculated measuring the relation between spindle density (represented by the ratio of spindles during stage 2 sleep) and memory performance. There was a positive relationship between spindle density and memory negative backgrounds, which was marginally significant $r(15) = 0.51$, $p=0.06$.

There were no other significant relationships between spindle density and memory performance (see Table 6 for all correlations).

Discussion

Overview of Findings

The primary aim of the present study was to investigate how visual distinctiveness and affective factors of emotion (valence and arousal) filter information for selective memory consolidation during sleep by determining the relation between different sleep stages and memory performance for distinctive and emotional information. It has previously been suggested that NREM sleep stages, and more specifically SWS sleep, are critical for episodic memory consolidation (Alger et al., 2012; Diekelmann et al., 2012; Gais & Born, 2004b; Peigneux et al., 2004; Rasch et al., 2007). Recent evidence also suggests that Stage 2 sleep may also enhance episodic memory (Fogel & Smith, 2006; Ruch et al., 2012). REM sleep, on the other hand, has been primarily implicated in processing of emotional information (Ackermann & Rasch, 2014; Groch et al., 2013; Nishida et al., 2009; van der Helm et al., 2011; Wagner et al., 2001). Moreover, it has been suggested that certain information is filtered (or 'tagged') during encoding and then selectively consolidated during sleep (Bennion et al., 2013; Oudiette et al., 2013; Payne & Kensinger, 2010; Saletin et al., 2011; Wilhelm et al., 2011). However the mechanism by which information is tagged for consolidation, and the role sleep may have in mediating that process is unknown.

Using a similar memory trade-off paradigm to previous studies (Kensinger et al., 2007), participants were presented with pictures of scenes consisting of a target item (either negative, positive, neutral, or distinctive but emotional neutral) superimposed over neutral indoor and outdoor background scenes. After a 2-hour interval, which included either a nap or an equivalent period of wakefulness, participants were given a surprise recognition test on the items and backgrounds separately. Previous research suggests that when comparing negative and neutral scenes, the magnitude of memory trade-offs is enhanced after a full night of sleep (Payne et al., 2008). Overall benefits in emotional memory performance (again comparing negative to neutral) are also observed after a shorter sleep session, such as a 90 minute nap (Nishida et al., 2009). Moreover, within the laboratory it has been demonstrated that negative and positive emotion, and distinctiveness were factors which could elicit memory trade-offs of the same magnitude (Campanella & Hamann, in preparationa, in preparationb). Thus, it was predicted that memory trade-offs for negative, positive, and distinctive scenes would be enhanced after a two-hour nap. Contrary to what was predicted, there were no differences in the magnitude of the memory trade-off effect (measured by an enhancement in recognition memory for items in the experimental condition compared to the neutral condition and a corresponding decrease recognition memory for backgrounds paired with items in the experimental condition compared to backgrounds paired with neutral items). Instead, there was a non-significant trend towards an enhancement in memory for items after the nap, with significant enhancements in recognition memory for neutral items after a nap. There was also a weak benefit in corrected recognition performance for negative items after a nap. In addition, there were correlations between different aspects of sleep, more specifically time spent sleeping and memory for distinctive items, and Stage 2 sleep and memory for positive items. There were also non-significant for spindle density and memory for negative backgrounds. SWS and REM sleep had little effect on subsequent recognition performance in the current study. Thus, the present study suggests that although there are some selective benefits to memory after a period of sleep, though they are not reflected in the memory trade-off effect. Instead, they seem to be restricted to enhancing memory the central items and in particular, for neutral items, though perhaps to a lesser extent, negative items. Moreover, it appears that based on the correlations between the different sleep stages and memory for different components of emotional, distinctive, and neutral scenes that emotional, distinctive and neutral information may be consolidated during sleep. The behavioral and correlational findings will be addressed in the next sections separately.

Behavioral Benefits Of A Nap On Recognition Performance

The present study used a modified memory trade-off paradigm, which was originally utilized by Payne et al, (2008, 2011) because it was designed to measure memory performance for salient/thematically relevant information and background information separately; thus providing a more sensitive measure of selectivity than using emotionally evocative images (Hu et al., 2006). The present study differed from the studies conducted by Payne et al (2008, 2011) in that the comparison was between negatively arousing, positively arousing, visually distinctive but emotionally neutral, and neutral conditions, as opposed to just comparing negative arousing composite scenes to neutral composite scenes. In addition, the present study utilized a shorter interval with a 2-hour polysomnography-recorded nap instead of an overnight behavioral paradigm with a 12-hour interval. Although there were overall memory trade-offs for all experimental conditions in the present study, there was no difference in the magnitude of the trade-off between interval conditions,. This lack of preferential enhancement after sleep did not support previous studies, during which Payne et al (2008, 2011) reported enhancements in memory trade-offs after a period of sleep. Instead, the present study observed selective benefits in recognition memory for only neutral items after a nap, although there was a clear trend of sleep benefiting memory for negative items (p = 0.08). There were no corresponding decreases in memory for backgrounds paired with these conditions. Moreover, positive and distinctive item memory showed no overall benefit after a nap. The pattern also persisted when taking into account the participant's confidence in their response. In sum, there was a selective benefit for neutral items, which may also extend to negative with more statistical power. Memory for positive and distinctive items, on the other hand, did not appear to benefit from sleep. The lack of a selective memory trade-off may call into question whether any memory benefits are in fact a result of sleep actively consolidating memory and are not due to passive protection from interference during wakefulness. However, the fact that memory is selectively enhanced for neutral and possibly negatively arousing central items after sleep, with no corresponding change in memory for any of the backgrounds, suggests that sleep is actively mediating consolidation.

The current findings therefore suggest—at least after a nap—that sleep benefits memory for neutral items, and perhaps, to a lesser, extent negative items. The enhancement of neutral information is particularly interesting as it does not match previous findings of studies, which suggest that sleep will preferentially enhance emotional information (Payne et al., 2008; Payne & Kensinger, 2010, 2011a; Wagner et al., 2001). Moreover it does not support the idea that memory enhancements after sleep will be strongest for information which is important or salient (Payne & Kensinger, 2010;

Saletin et al., 2011; Wilhelm et al., 2011), as one would assume that neutral information, which showed the strongest benefit from sleep in the current study, is not naturally salient. It is possible that the differences observed in the present study may be due to differences in experimental paradigms across this literature. Studies investigating the effects of sleep on emotional memory consolidation vary in stimuli content (pictures, composite scenes, faces, and text), presentation time, and the array in valence and arousal. Thus it is difficult to directly compare findings. However, it is important to note that Hu et al, (2006) failed to find a preferential memory benefit for negatively arousing stimuli relative to neutral stimuli for 'Remember' judgments (described as the conscious *recollection* of vivid contextual details, such as "when" information was learned and may require a deeper level of processing). Instead, the preferential benefit for emotional stimuli was for 'Know' judgments (described as a feeling of *familiarity* for a stimulus, which is sensation of having seen it before but not knowing why). The findings of the current study, therefore, support Hu et al's. 'Remember' response findings. It is important to note, however, that the recognition test was different between studies and so direct comparisons between studies may not work. The results of the current study are also supported by two recent overnight sleep paradigm studies, which also failed to find a preferential benefit for emotionally arousing pictures (Baran et al., 2012) and composite scenes (Lewis et al., 2011), and thus also observed benefits for neutral information. Finally, a study investigating the effects of sleep deprivation on consolidation of emotional and neutral information demonstrated that impairments in memory were more pronounced for neutral information. In fact, emotional information, and especially negatively arousing information, was relatively well protected after a period of sleep deprivation (Atienza & Cantero, 2008), suggesting that neutral information may also be sensitive to benefits of sleep.

It is also important to note that sleep benefits have been observed when only using neutral stimuli (Alger et al., 2012; Diekelmann et al., 2012; Ellenbogen et al., 2006; Gais & Born, 2004a; Gais, Mölle, Helms, & Born, 2002; Oudiette et al., 2013; Payne et al., 2012; Rasch et al., 2007; Rauchs et al., 2011; Rudoy et al., 2009; Saletin et al., 2011; Wilhelm et al., 2011). However, a majority of the sleep studies mentioned above utilize intentional memory paradigms and one could argue that emotion could add intentionality to incidental encoding (Wilhelm et al., 2011), which would in turn selectively increase memory for emotional information. It is important, therefore, to determine what processing may occur to result in the sleep benefit to neutral central items.

One possible explanation could come from Oudiette et al's (2013) study investigating the effect of sleep in benefitting high and low rewarded information using a targeted-reactivation paradigm. Although the stimuli were not emotional, it was still considered salient as participants were rewarded for their participation. In the study they found that cueing benefited all low-value associations (whether the cue was presented during sleep or not) in the sleep group, whereas it only benefitted cued associations in the wake group. Furthermore, high-value associations received no benefit from sleep, which is surprising in light of previous findings that sleep selectively benefits salient information (Saletin et al., 2011; Wilhelm et al., 2011). Oudiette and colleagues (2013) speculated that in the context of rewarded learning, that wakefulness might contribute to the consolidation of salient memories. This idea is confirmed in a spatial navigation study in rats conducted by Singer and Frank, (2009), during which they demonstrated that rewarded outcomes enhanced waking reactivation of paths associated with a reward during learning. In addition, it has been demonstrated that the amount of reactivation of goal-related patterns predicted later memory performance regardless of whether reactivation occurred during the acquisition phase or during the subsequent rest phase. These findings suggest that both online and offline reactivation can strengthen salient memories (Dupret et al., 2010). Thus, in the context of the current study, it is possible that the most salient information—that is the emotional and distinctive central items—was equally reactivated during wake and sleep intervals, whereas the lower value information (i.e., the neutral central items) was only reactivated during sleep resulting in the significant boost in memory after sleep.

As noted earlier, negative items showed marginally significant memory benefits, which suggest that sleep may also preferentially benefit some emotional information. Therefore, in the context of the previous theory, it is possible that the distinctive stimuli, which were also novel to participants (in that many of the stimuli were chimeric images of imaginary objects and creatures), were viewed as the most salient and thus equally reactivated during sleep and wakefulness. The emotional and neutral items, on the other hand, may be preferentially consolidated during sleep due to processes of generalization and abstraction, which are said to promoted during sleep (Gómez et al., 2006; Lau et al., 2011; Wagner et al., 2004). The emotional and neutral items all shared the common rule of being objects that could be readily identified and labeled and it is possible that sleep may facilitate the reorganization of discrete memory traces into a flexible relational network of items linked by their common rule, and ultimately reinforce memory for the entire memory domain. Alternatively, as there was a marginal benefit for all items (*p*=

0.06) it is possible that the central items were selected for preferential consolidation during sleep based on the general rule of all being items against a background. This latter explanation seems more likely as there was no significant interaction between interval group and item category.

An alternate explanation for the differential benefits of memory after sleep may be a result of differential processing at encoding. Although evidence suggests that emotional (Christianson et al., 1991; Mickley Steinmetz et al., 2013; Riggs et al., 2011) and distinctive (Blackford et al., 2010; Itti & Baldi, 2009; Mitchell et al., 1998; Pickel, 1998; Ranganath & Rainer, 2003) both attract attentional resources (Campanella & Hamann, in preparationa), it is possible that emotional informational information may also undergo additional post encoding processes including rumination and elaboration (Christianson, 1992; Kensinger & Corkin, 2004; Talmi & Moscovitch, 2004). Thus, it is possible that these additional processes could help filter information for preferential consolidation. The problem with this explanation, however, is that it does not explain the preferentially memory enhancement for neutral stimuli but does support the theory that sleep may consolidate emotional and neutral information equally (Baran et al., 2012). It is also possible that what determines what information is salient and worthy of increased attentional and cognitive processing is flexible and context-dependent. For example, in the current study there were 4 different categories; negative, positive, distinctive, and neutral, compared to previous studies, which just compared an emotional condition to neutral. The addition of the extra two categories may change what is considered ‘salient’ and what will receive preferential consolidation during sleep. In the current study, the neutral condition may be considered the oddball in that objects do not inherently attract more attention. Thus, participants may ruminate more over the neutral scenes resulting in selective consolidation during sleep. What is clear is that more research is needed to examine how each of the conditions were processed to determine what features will ultimately be selectively consolidated.

Correlation Between Components Of Sleep and Subsequent Memory Performance

One of the primary goals of the current study was to investigate the role of different physiological correlates of sleep in mediating memory consolidation for emotional and distinctive composite scenes. Sleep stages were recorded using polysomnography and correlations were conducted between each of the different sleep stages and memory for each of the scene components in the 4 different categories. A correlation between the time spent sleeping and memory performance was also conducted as it has been suggested that the duration of sleep also benefits episodic memory (Diekelmann et al., 2012). For both positive and distinctive items there was strong positive relation between the time an individual spent sleeping and corrected recognition performance. In the case of positive items, however, the relation was marginal (p=0.06). What is interesting is that behaviorally there appeared to be less of a sleep benefit for positive and, to a greater extent, distinctive item memory and yet these two categories showed the greatest memory boost the longer an individual slept. Taken together, this suggests is that perhaps the passage of time, and not sleep necessarily, may be important for reactivation of positive and distinctive item memories. When calculating sleep duration time in Stage 1 was included, which does not necessarily correspond with memory enhancements. More specifically, Stage 1 sleep is a short transitional state between wakefulness and sleep (Carskadon et al., 2000) and thus likely not implicated in sleep-dependent sleep consolidation (Stickgold, 2005). As a result the total amount of time an individual spends sleeping is not sufficient to determine whether sleep is playing an active role in memory consolidation. Studies which have shown increasing benefits on memory the longer an individual spends sleeping have usually found additional positive correlations between memory performance and a particular stage of sleep, such as SWS (Diekelmann et al., 2012). Interestingly, however, in the current study there were no relations between SWS and memory performance, which does not support previous findings (Alger et al., 2012; Diekelmann et al., 2012; Gais & Born, 2004b; Peigneux et al., 2004; Rasch et al., 2007; Rudoy et al., 2009; Wilhelm et al., 2011). However it is important to note that only ten of the fifteen participants reach SWS during the napping period. Therefore there may not be sufficient power to measure a relationship between time in SWS and subsequent memory performance.

Another NREM stage of sleep is Stage 2, and there is increasing evidence to suggest that there is a positive relation between both duration of Stage 2 and spindle density and subsequent memory performance (Fogel & Smith, 2006; Gais et al., 2002; Ruch et al., 2012; Schabus et al., 2004). Spindle density can be calculated both manually and automatically and is a measurement of the number of spindles per minute. There was a positive relation between memory for negative backgrounds and both duration Stage 2 sleep, which was marginal (p=0.09), and spindle density, which also was marginal (p=0.06), which may reflect general enhancements in neutral memory performance, as the backgrounds themselves are neutral; which supports previous evidence which demonstrated positive correlations between neutral verbal memory performance and both Stage 2 duration and spindle density (Fogel & Smith, 2006; Gais et al., 2002; Schabus et al., 2004). Interestingly, however, there was a strong a positive correlation between Sleep 2 duration and memory for positive items, which did not also show an equivalent correlation between memory and spindle density, but nevertheless suggests a possible mechanism involved in consolidation of positive items. It is possible that the duration in Stage 2 is sufficient to consolidate positive items, but it is also possible that the correlation may reflect the relation between memory performance and the general duration of time during which memory is protected from interfering encoding processes as Stage 2 sleep typically takes up a higher portion of a nap. An interesting future analysis, which could not be conducted for this manuscript due to lack resources, would be to investigate the relationship between memory performance for positive items and sigma activity, a frequency band frequently associated with Stage 2 sleep and sleep spindles (Finelli, Borbély, & Achermann, 2001), which may be a more sensitive measure for investigating the role of Stage 2 in memory consolidation than duration.

Finally, there was no relation between time spent in REM sleep and memory performance for any of the components of the scenes. It is important to note, however, that only twelve of the fifteen participants were included in this analysis, as three individuals did not achieve REM sleep during the nap period, thus reducing statistical power. In addition, participants on average spent approximately 14 minutes in REM sleep, which is considerably less than studies, which use an overnight paradigm (Wagner et al., 2001) and thus experience more REM to process emotional stimuli.

Conclusion

In summary, the current study aimed to investigate the role of visual distinctiveness and affective factors of emotion (valence and arousal) in filtering information for selective memory consolidation during sleep. This aim was accomplished by determining the relation between different characteristics of sleep and memory trade-offs for distinctive and emotional information. It was hypothesized that memory trade-offs for emotional and distinctive composite scenes would be enhanced after a nap, compared to an equivalent period of wakefulness. Contrary to what was hypothesized, there was no enhancement in memory trade-offs for either distinctive or emotional scenes after sleep. Instead, there was a general not significant enhancement for the salient central items of all the composite scenes and, more specifically, a significant increase in memory for neutral items after sleep. There was also a marginal enhancement for negative items after sleep. Behavioral benefits for neutral item memory were supported with not-significant correlations with Stage 2 sleep and spindle density neutral backgrounds and memory for backgrounds originally paired with negative items (which is also neutral information), suggesting that Stage 2 sleep may influence consolidation of neutral stimuli. Stage 2 sleep, however, may also mediate consolidation of positive items, and thus be responsible for strengthening of some emotional information. Distinctive items showed a positive relationship with sleep duration, thus tentatively suggesting that distinctive information may be consolidated during sleep. The findings also illustrate the importance of investigating the effect that different components of sleep have on mediating memory consolidation for emotional, neutral, and distinctive information.

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Tables

Table 1

Demographic information for Nap-Interval and Wake-Interval Conditions

	Group				
	Sleep		Wake		Difference
Test	*M*	*SEM*	*M*	*SEM*	*P*
Age	20.47	2.97	20.60	2.26	0.84
Average Sleep	7.38	0.35	7.78	0.16	0.29
Epworth Score	10.07	1.00	9.36	0.72	0.57
Stanford Sleepiness Scale	2.57	0.23	3.10	0.24	0.17

Table 2

Mean subjective arousal and distinctiveness ratings for all items

	Rating			
	Arousal		Distinctiveness	
Category	*M*	*SEM*	*M*	*SEM*
Negative	3.06	0.15	2.40	0.12
Positive	2.69	0.12	1.60	0.09
Distinctiveness	2.03	0.13	4.13	0.11
Neutral	1.49	0.09	1.68	0.08

Note: Subjective arousal and distinctiveness ratings were calculated on a 5 point Likert-scale (1= low to 5= high). For arousal ratings all categories differed from each other at $p < 0.005$. For distinctive ratings, all categories differed from each other at $p < 0.005$ except for positive and neutral items.

Table 3

Recognition Performance for Nap and Wake Interval Groups

	Group			
	Nap-interval (N=15)		Wake-interval (N=15)	
Memory Type	*M*	*SEM*	*M*	*SEM*
Hits for Items				
Negative	0.90	0.02	0.87	0.03
Positive	0.83	0.03	0.80	0.04
Distinctive	0.80	0.03	0.82	0.03
Neutral	0.83	0.03	0.78	0.04
False Alarms for Items				
Negative	0.14	0.02	0.23	0.05
Positive	0.11	0.03	0.20	0.04
Distinctive	0.09	0.02	0.20	0.05
Neutral	0.16	0.02	0.29	0.05
Corrected Recognition for Items				
Negative	0.75	0.03	0.64	0.05
Positive	0.72	0.04	0.60	0.06
Distinctive	0.71	0.04	0.62	0.06
Neutral	0.67	0.05	0.49	0.06
Hits for Backgrounds				
Negative	0.49	0.04	0.56	0.05
Positive	0.50	0.04	0.58	0.04
Distinctive	0.44	0.04	0.54	0.05
Neutral	0.58	0.05	0.61	0.05
False Alarms for Background				
Negative	0.20	0.03	0.30	0.05
Positive	0.23	0.04	0.28	0.04
Distinctive	0.25	0.03	0.25	0.04
Neutral	0.22	0.04	0.29	0.03
Corrected Recognition for Backgrounds				
Negative	0.29	0.04	0.26	0.07
Positive	0.28	0.05	0.30	0.04
Distinctive	0.20	0.05	0.29	0.06
Neutral	0.37	0.05	0.32	0.04

Note. Corrected recognition performance was calculated by subtracting proportion of false alarms from proportion of hits. Backgrounds were always neutral and are designated to each experimental category (negative, positive, distinctive, and neutral) by the central item that was originally paired with that background.

Table 4

Recognition Performance for High Confidence Nap and Wake Interval Groups

	Group			
	Sleep-interval (N=15)		Wake-interval (N=15)	
Memory Type	*M*	*SEM*	*M*	*SEM*
Hits for Items				
Negative	0.86	0.03	0.80	0.04
Positive	0.75	0.04	0.70	0.05
Distinctive	0.71	0.04	0.71	0.05
Neutral	0.73	0.04	0.64	0.05
False Alarms for Items				
Negative	0.08	0.02	0.11	0.02
Positive	0.04	0.01	0.11	0.03
Distinctive	0.05	0.01	0.08	0.02
Neutral	0.07	0.02	0.12	0.03
Corrected Recognition for Items				
Negative	0.78	0.03	0.69	0.05
Positive	0.71	0.04	0.59	0.06
Distinctive	0.66	0.04	0.63	0.06
Neutral	0.67	0.05	0.52	0.06
Hits for Backgrounds				
Negative	0.32	0.04	0.16	0.04
Positive	0.32	0.04	0.16	0.04
Distinctive	0.31	0.04	0.37	0.05
Neutral	0.42	0.04	0.42	0.04
False Alarms for Background				
Negative	0.05	0.01	0.12	0.02
Positive	0.08	0.02	0.14	0.04
Distinctive	0.07	0.02	0.10	0.03
Neutral	0.12	0.02	0.12	0.03
Corrected Recognition for Backgrounds				
Negative	0.27	0.04	0.24	0.05
Positive	0.24	0.05	0.31	0.05
Distinctive	0.24	0.05	0.27	0.06
Neutral	0.36	0.05	0.30	0.04

Note. Corrected recognition performance was calculated by subtracting proportion of false alarms from proportion of hits. Backgrounds were always neutral and are designated to each experimental category (negative, positive, distinctive, and neutral) by the central item that was originally paired with that background.

Table 5

Breakdown of sleep stages during nap period

Sleep Measure	*M*	*SEM*
Sleep Duration (min)	81.97	6.92
Time in Wake (min)	36.12	6.73
Time in Stage 1 (min)	10.07	1.52
Time in Stage 2 (min)	39.73	4.56
Time in Stage 3 (min)	18.17	4.49
Time in REM Sleep (min)	14.00	3.70
Stage 1 (%)	17.00	6.00
Stage 2 (%)	49.00	5.00
Stage 3 (%)	19.00	5.00
REM Sleep (%)	15.00	4.00

Note. Percent of time in each sleep stage was calculated by dividing total sleep duration from the time spent in each corresponding sleep stage.

Table 6

Correlations between sleep measures and corrected recognition memory performance

	Time Asleep (N=15)	**Time in Stage 1 (N=15)**	**Time in Stage 2 (N=14)**	**Time in Stage 3 (N=10)**	**Time in REM Sleep (N=12)**	**Spindle Ratio (N=15)**
Negative Objects	-.198	.207	-.245	.136	.278	-.232
Positive Objects	**.499***	-.151	**.557****	.005	.046	.073
Distinctive Objects	**.609****	-.224	.329	-.269	.458	.145
Neutral Objects	.327	-.075	.257	-.037	.356	-.043
Negative Backgrounds	.340	**-.500***	**.454***	-.106	-.052	**.505***
Positive Backgrounds	-.079	.216	-.018	-.087	-.021	-.044
Distinctive Backgrounds	-.099	-.017	-.156	.169	.068	-.027
Neutral Backgrounds	.285	-.227	.225	-.030	.201	.427

Note: ** denotes $p < 0.05$, * denotes $p < 0.10$

Figures

Negative

Positive

Distinctive

Neutral

Figure 1: Example of a composite scene from each category. Reflects four different counterbalancing lists. It is important to note that each participant only saw each background once during the encoding session.

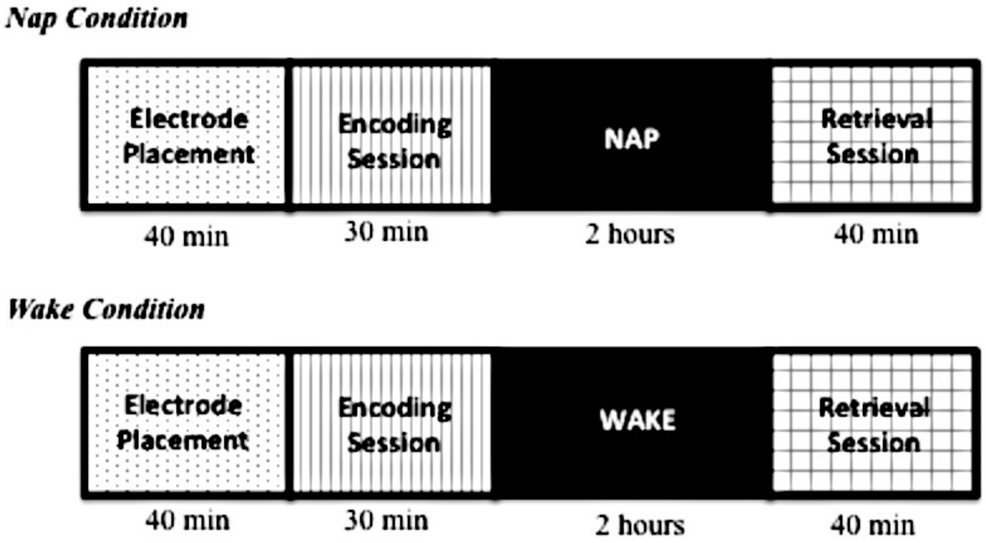


Figure 2: Nap Paradigm.

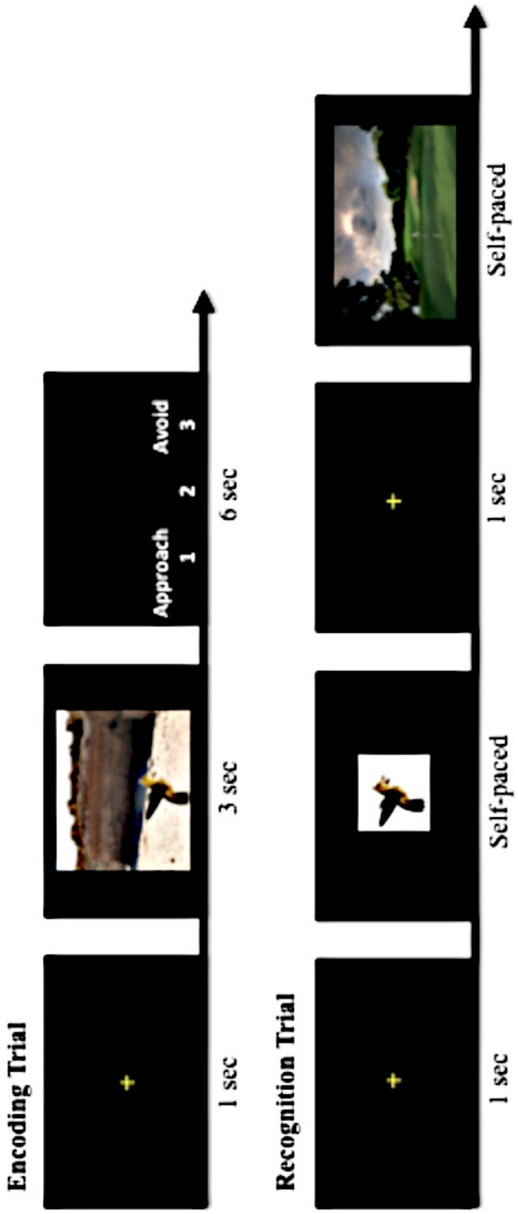


Figure 3: Example of Encoding and Recognition Trials. For recognition trial, there is an example of an OLD item and a NEW background. During recognition trial, participants were instructed to mark their responses on a 1-6 confidence scale (1 = Definitely New, 2 = Probably New, 3 = Maybe New, 4 = Maybe Old, 5 = Probably Old, 6 = Definitely Old)

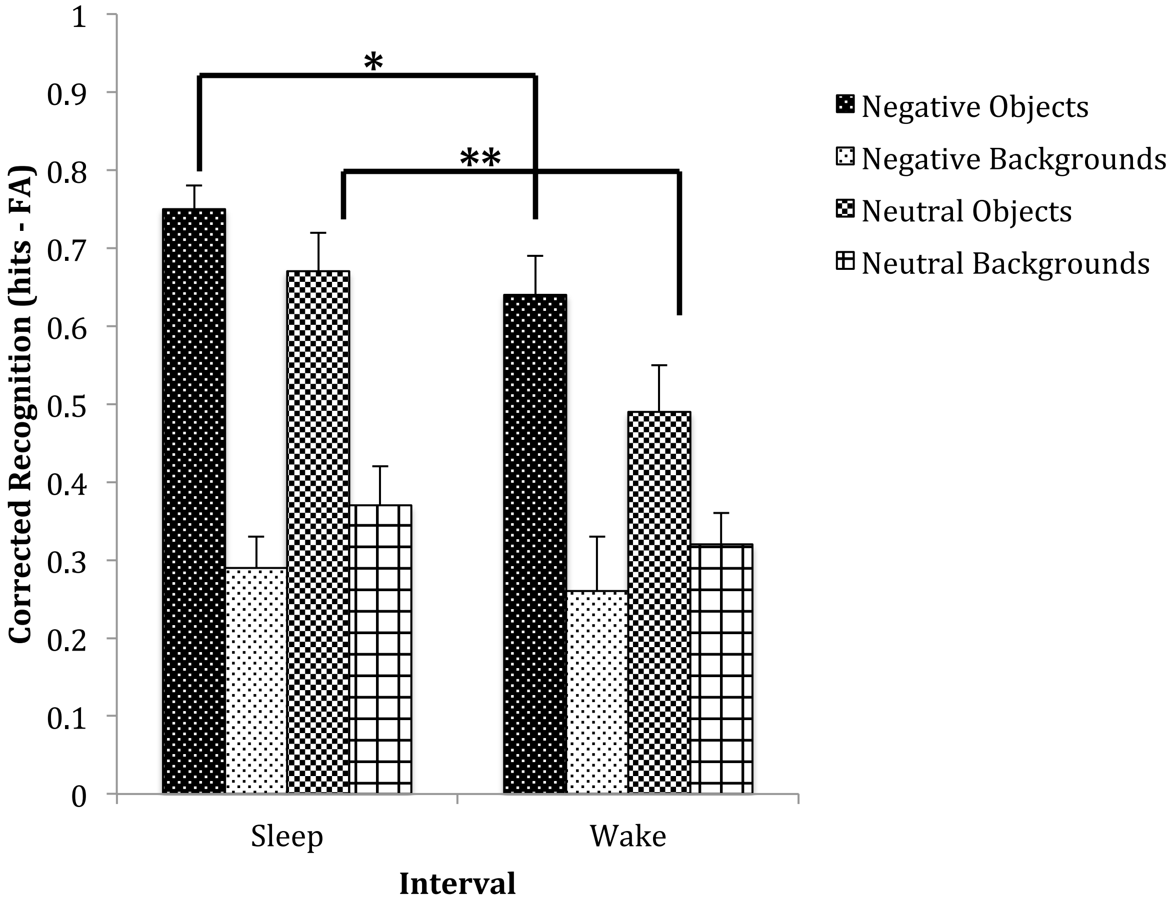


Figure 4: Memory trade-off performance for negative scenes for nap-interval and wake-interval conditions. * $p< 0.10$, ** $p< 0.05$

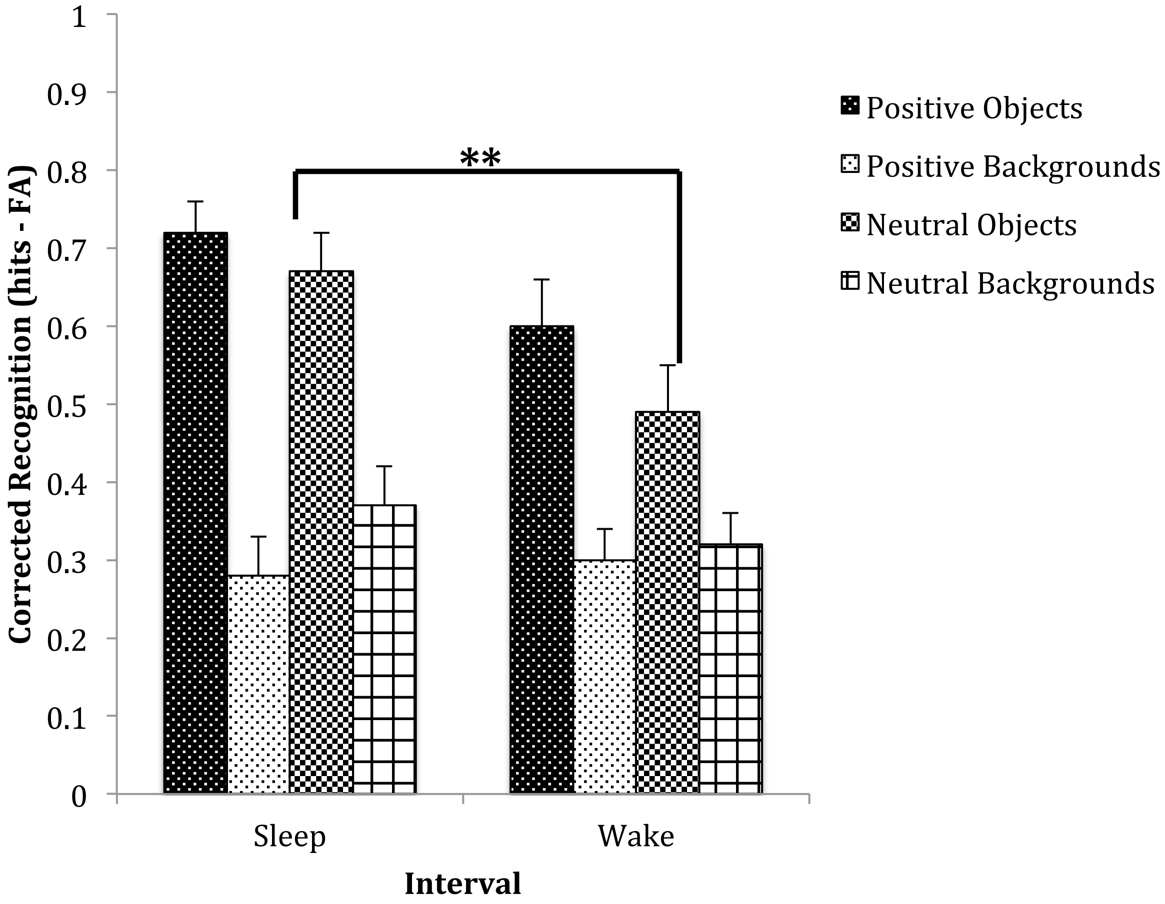


Figure 5: Memory trade-off performance for positive scenes for nap-interval and wake-interval conditions. *$p < 0.05$

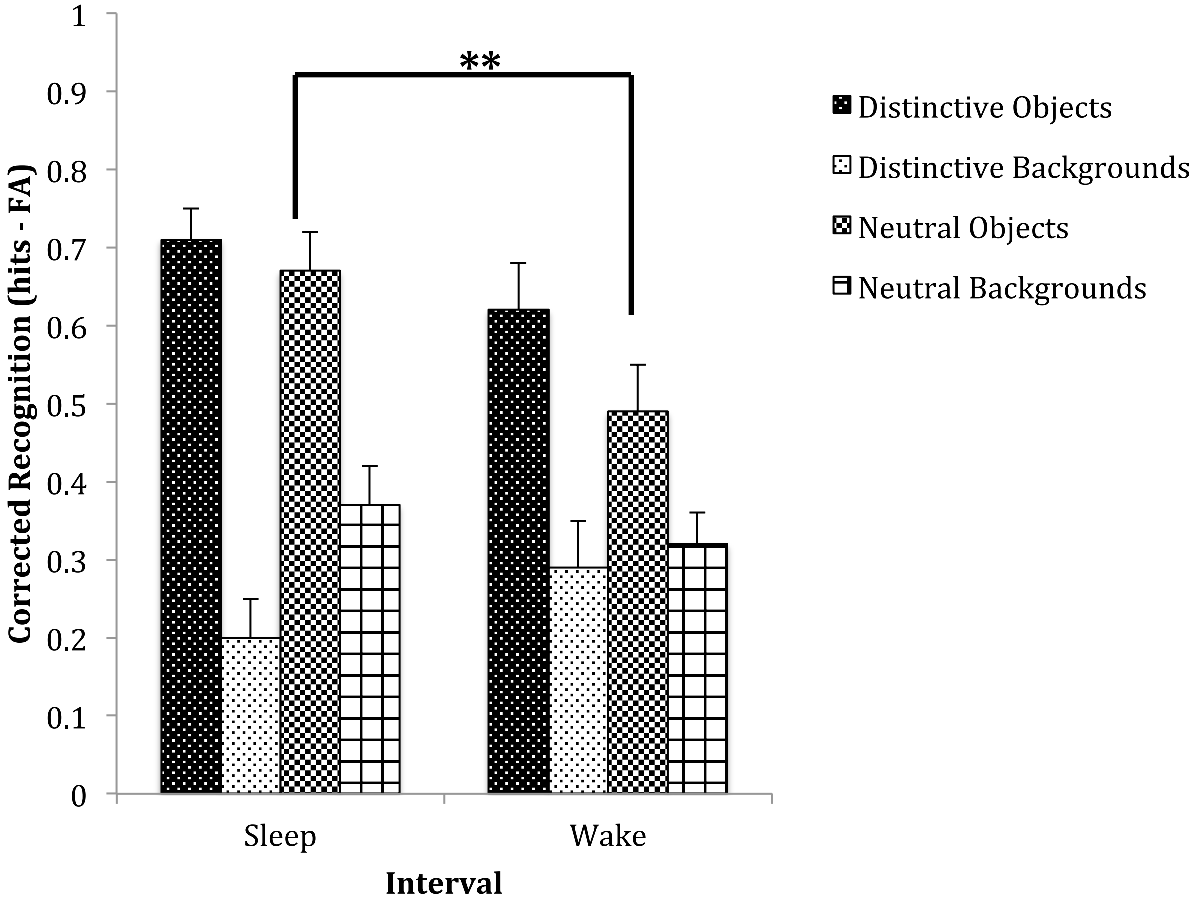


Figure 6: Memory trade-off performance for distinctive scenes for nap-interval and wake-interval conditions.

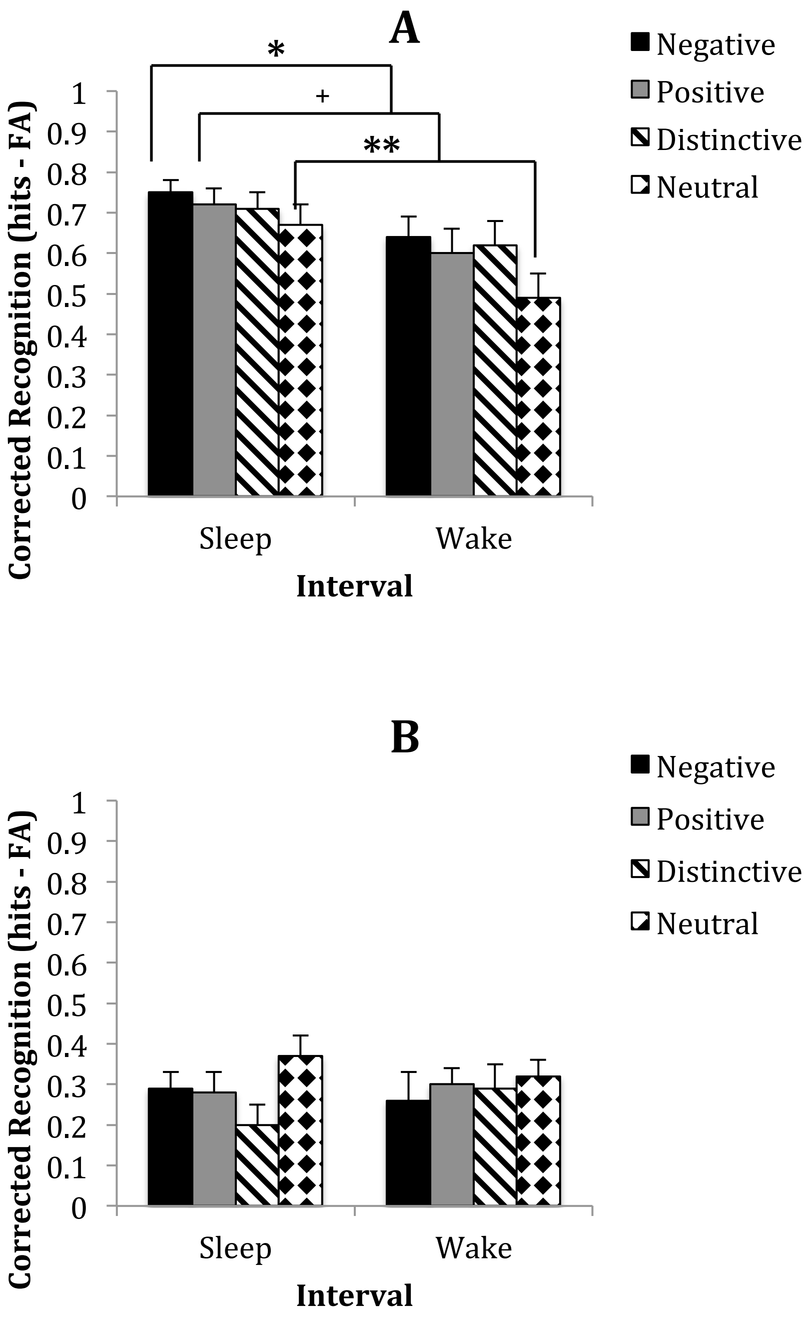


Figure 7: Corrected recognition performance for nap-interval and wake-interval conditions. A) Item Memory. B) Background Memory. **$p< 0.05$, *$p< 0.10$, $^{+}p<0.15$

Appendix 1

Example of Epworth Sleepiness Scale (Johns, 1991)

Epworth Sleepiness Scale

How likely are you to doze off or fall asleep in the following situations, in contrast to just feeling tired? This refers to your usual way of life in recent times. Even if you have not done some of these things recently, try to work out how they would have affected you. Use the following scale to choose the **most appropriate number** for each situation

0 = would **never** doze
1 = **slight** chance of dozing
2 = **moderate** chance of dozing
3 = **high** chance of dozing

Situation *Chance of Dozing*

Sitting and reading………………………………………………______________________

Watching TV……………………………………………………._______________________

Sitting, inactive, in a public place (e.g., a theater or a

meeting)……………………………………………………..…..______________________

As a passenger in a car for an hour without a

break………………………………………………………………_______________________

Lying down to rest in the afternoon when circumstances

permit…………………………………………………………...…______________________

Sitting and talking with someone…………………………….______________________

Sitting quietly after a lunch without alcohol………………….______________________

In a car, while stopped for a few minutes in traffic………….._____________________

Example of Stanford Sleepiness Scale (Hoddes et al., 1972)

Stanford Sleepiness Scale

Instructions: Please rate how alert you feel right now by circling one of the options:

Degree of Sleepiness	**Scale Rating**
Feeling active, vital, alert, or wide awake	1
Functioning at high levels, but not at peak; able to concentrate	2
Awake, but relaxed; responsive but not fully alert	3
Somewhat foggy, let down	4
Foggy; losing interest in remaining awake; slowed down	5
Sleepy, woozy, fighting sleep; prefer to lie down	6
No longer fighting sleep, sleep onset soon; having dream-like thoughts	7

Appendix 2

Supplemental analyses for general memory trade-off performance, which was defined by ‘4’, ‘5’, and ‘6’ old responses on the 1-6 confidence scale.

Examining Differences In Memory Trade-offs Between Sleep And Wake Groups For Negative, Positive, And Distinctive Composite Scenes

Memory trade-off effects

Based on strong a priori hypotheses that sleep would enhance memory trade-offs for emotional and distinctive scenes, three separate repeated-measures ANOVAs with category (experimental category, neutral) and scene component (item, background) were conducted. Each of the experimental conditions (negative, positive, and distinctiveness) was compared to neutral. For each of these repeated-measures ANOVAs, interval group (nap, wake) was a between-subjects factor. For the negative category, there was a significant main effect for interval group; $F(1, 28) = 4.36$, $p = 0.05$, $\eta_G^2 = 0.13$, but there was not a significant main effect for category; $F(1, 28) = 1.30$, $p = 0.27$, $\eta_G^2 = 0.04$. There was a significant main effect for scene component; $F(1, 28) = 49.06$, $p < 0.005$, $\eta_G^2 = 0.63$. There was also a significant interaction between category and scene component; $F(1, 28) = 23.04$, $p < 0.005$, $\eta_G^2 = 0.45$, indicating that there was an overall memory trade-off. However, there were no significant interactions between interval group and category; $F(1, 28) = 0.78$, $p = 0.38$, $\eta_G^2 = 0.03$, nor between interval group and scene component; $F(1, 28) = 1.33$, $p = 0.26$, $\eta_G^2 = 0.02$. In addition, there was no three-way interaction between interval, category, and component; $F(1, 28) = 0.56$, $p = 0.46$, $\eta_G^2 = 0.01$ indicating that although there was a difference in overall memory performance between nap and wake interval groups, the difference does not appear to be in the trade-off effect (see Figure 4 in manuscript).

For the positive category, there was not a significant main effect for interval group; $F(1, 28) = 2.55, p = 0.12, \eta_G^2 = 0.08$, or a significant main effect for category; $F(1, 28) = 0.41, p = 0.53, \eta_G^2 = 0.01$, but there was a significant main effect for scene component; $F(1, 28) = 46.18, p < 0.005, \eta_G^2 = 0.60$. There was a significant interaction between category and scene component; $F(1, 28) = 14.40, p < 0.005, \eta_G^2 = 0.34$ indicating there was an overall memory trade-off. However, there were no significant interactions between interval group and category—although it did approach significance—$F(1, 28) = 3.12, p = 0.09, \eta_G^2 = 0.10$, nor between interval group and component; $F(1, 28) = 2.49, p = 0.13, \eta_G^2 = 0.03$. In addition, there was no three-way interaction between interval, category, and component; $F(1, 28) = 0.02, p = 0.89, \eta_G^2 = 0.00$ indicating that, although there is an overall trade-off for positive scenes it does not differ between nap and wake groups (see Figure 5 in manuscript).

Finally, for the distinctive category, there was not a significant main effect for interval $F(1, 28) = 1.29, p = 0.27, \eta_G^2 = 0.04$, or for category $F(1, 28) = 0.27, p = 0.61, \eta_G^2 = 0.01$, but there was a significant main effect for component $F(1, 28) = 50.37, p < 0.005, \eta_G^2 = 0.62$. There was also a significant interaction between category and component $F(1, 28) = 17.27, p < 0.005, \eta_G^2 = 0.38$, and interval and category $F(1, 28) = 7.61, p = 0.01, \eta_G^2 = 0.21$. The interaction between interval and component approached significance $F(1, 28) = 3.14, p = 0.09, \eta_G^2 = 0.04$. There was no three-way interaction between interval, category, and component $F(1, 28) = 0.40, p = 0.53, \eta_G^2 = 0.01$ indicating that although there are memory differences between distinctive and neutral categories between interval, these differences are not in the memory trade-off effect (see Figure 6 in manuscript).

Differences in the magnitude of the memory trade-off between nap and wake groups

In order to determine whether there might be a difference in the magnitude of a memory trade-off for either emotional or distinctive scenes after an interval that included either sleep or wakefulness, repeated-measures ANOVAs were conducted using difference scores. Difference scores were calculated by subtracting the neutral corrected recognition performance for items and backgrounds from the corrected recognition performance for the items and backgrounds in the three (negative, positive, and distinctive) experimental conditions (e.g., difference score for negative items = corrected recognition for negative items – corrected recognition for neutral items). The benefit of using differences scores for these comparisons is that the difference score provides a measure of the magnitude of difference between neutral, or the baseline, and the experimental condition, which can then be compared statistically with an ANOVA. A repeated-measures ANOVA with interval (nap, wake) as the between-subjects factor and category (negative, positive, and distinctive) and scene component (item, background) as within-subjects factors did not result in a significant main effect for interval group; $F(1, 28) = 0.003$, $p = 0.96$, $\eta_G^2 = 0.00$, category $F(2, 56) = .60$, $p = 0.55$, $\eta_G^2 = 0.02$, or scene component $F(2, 56) = 0.28$, $p = 0.60$, $\eta_G^2 = 0.01$. There was also no significant interaction between category and scene component $F(2, 56) = 1.25$, $p = 0.29$, $\eta_G^2 = 0.04$ or between interval group and category; $F(2, 56) = 0.62$, $p = 0.54$, $\eta_G^2 = 0.02$. There was a significant interaction between interval group and scene component; $F(2, 56) = 5.54$, p

= 0.06, $\eta_G^2 =$ 0.04 suggesting there was a difference in difference scores for items and backgrounds between interval groups. There was no significant three-way interaction between interval, category, and component $F(2, 56) = 1.68$, $p = 0.20$, $\eta_G^2 = 0.01$, suggesting although there might be a difference in memory trade-off magnitude between categories, it did differ whether a participant napped or not.

Planned comparison independent t-tests examining interval conditions confirmed that there was no significant difference between interval conditions for magnitude of memory differences for negative items; $t(28) = -1.33$, $p =0.20$, negative backgrounds; $t(28) = 0.11$, $p = 0.91$, positive items; $t(28) = -1.27$, $p = 0.21$, positive backgrounds; $t(28) = 1.20$, $p = 0.24$, and distinctive objects; $t(28) = -1.54$, $p =0.13$. There was, however, a significant increase in the difference score for distinctive backgrounds after a interval that did not include a nap; $t(28) = 2.16$ $p =0.04$.

Appendix 3

Supplemental analyses for high-confidence memory trade-off performance, which was defined by ‘5’ and ‘6’ old responses on the 1-6 confidence scale.

Examining Differences In Memory Trade-offs Between Nap And Wake Groups For Negative, Positive, And Distinctive Composite Scenes

Memory trade-off effects

In addition to analyses of overall recognition performance, recognition performance for high-confidence responses was also analyzed (e.g., corrected recognition calculated using hits and false alarms corresponding to “5” and “6” confidence responses). A repeated-measures ANOVA with factors of interval group (nap vs. wake) as a between-subjects factor, and factors of category (negative, positive, distinctive, neutral) and scene component (item vs. background) as within-subjects factors was conducted. There was not a significant main effect for interval group $F(1, 28) = 1.18$, $p = 0.47$, $\eta_G^2 = 0.04$ or category $F(3, 84) = 2.12$, $p = 0.10$, $\eta_G^2 = 0.06$, but there was a significant main effect of scene component $F(1, 28) = 80.64$, $p < 0.005$, $\eta_G^2 = 0.73$. There was a significant interaction between category and scene component $F(3, 84) = 20.01$, $p < 0.005$, $\eta_G^2 = 0.24$ indicating that there was a memory trade-off, and a significant interaction between interval group and category $F(3, 84) = 3.41$, $p = 0.02$, $\eta_G^2 = 0.10$. However, there was no significant interactions between interval group and scene component $F(1, 28) = 1.43$, $p = 0.24$, $\eta_G^2 = 0.01$ and no three way interaction between interval group, category, and scene component $F(3, 84) = 0.91$, $p = 0.44$, $\eta_G^2 = 0.02$ indicating that although there were differences in memory performance between nap and wake interval groups, the different components that make up a memory trade-off did not differ between nap and wakefulness.

Planned comparison paired t-tests were conducted and revealed that corrected recognition for negative items was significantly higher than neutral items; $t(29) = 6.60$, $p < 0.005$, as were positive items; $t(29) = 2.58$, $p = 0.02$. There was no significant difference in memory for distinctive items between nap and wake interval groups, although it was marginal; $t(29) = 1.83$, $p = 0.08$. Planned comparison paired t-tests where interval group was collapsed also confirmed that corrected recognition for backgrounds paired with negative items was significantly lower than backgrounds paired with neutral items; $t(29) = -2.83$, $p = 0.01$, as were backgrounds paired with distinctive items; $t(29) = -2.59$, $p = 0.02$. Backgrounds paired with positive items, however, were not significantly lower than backgrounds paired with neutral items; $t(29) = -1.88$, $p = 0.07$, although it approach significance. These results confirm that memory trade-offs occur for negatively arousing stimuli, due to both enhanced memory for negative items and reduced memory for negative backgrounds.

Due to strong a priori hypotheses that there would be enhanced memory trade-offs for emotional and distinctive scenes after a nap, we conducted three separate repeated-measures ANOVAs with category (experimental category, neutral) and component (item, background), comparing each of the experimental conditions (negative, positive, and distinctiveness) to neutral. For each of these repeated-measures, interval (nap vs. wake) was a between-subjects factor. For the negative category, there was not a significant main effect for interval group, although it was marginally significant, $F(1, 28) = 3.83$, $p = 0.06$, $\eta_G^2 = 0.12$ or for category $F(1, 28) = 2.80$, $p = 0.11$, $\eta_G^2 = 0.09$, but there was a significant main effect for scene component $F(1, 28) = 76.51$, $p < 0.005$, $\eta_G^2 = 0.73$. There was also a significant interaction between category and scene component $F(1, 28) = 48.42$, $p < 0.005$, $\eta_G^2 = 0.63$. However, there were no significant interactions between interval group and category $F(1, 28) = 1.41$ $p = 0.25$, $\eta_G^2 = 0.13$, nor between interval group and scene component $F(1, 28) = 0.79$, $p = 0.38$, $\eta_G^2 = 0.01$. In addition, there was no three-way interaction between interval group, category, and scene component $F(1, 28) = 0.10$, $p = 0.75$, $\eta_G^2 = 0.05$ indicating that, although there is an overall trade-off for negative scenes it does not differ between nap and wake groups. There was however, an overall difference in memory performance between nap and wake groups (Figure 1S).

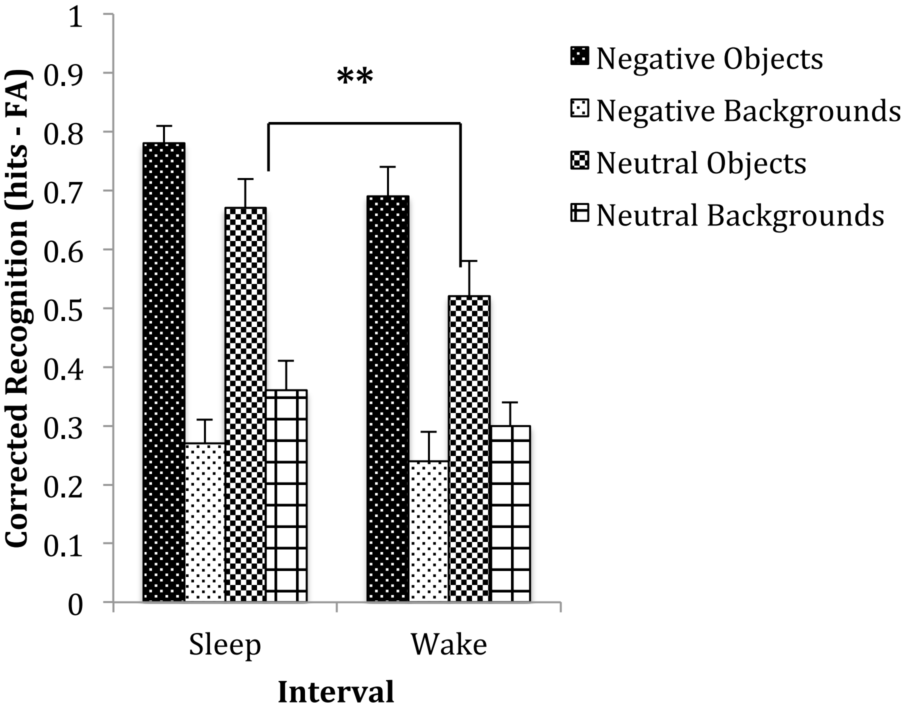


Figure 1S: Memory trade-off performance for high confidence responses for negative scenes for nap-interval and wake-interval conditions. $^{**}p \leq 0.05$

For the positive category, there was not a significant main effect for interval group $F(1, 28) = 1.77$, $p = 0.19$, $\eta_G^2 = 0.06$ or for category $F(1, 28) = 0.002$, $p = 0.97$, $\eta_G^2 =$

0.00, but there was a significant main effect for scene component $F(1, 28) = 52.77$, $p < 0.005$, $\eta_G^2 = 0.63$. There was also a significant interaction between category and scene component $F(1, 28) = 11.86$, $p = 0.002$, $\eta_G^2 = 0.28$, but not between interval group and category $F(1, 28) = 0.03$, $p = 0.86$, $\eta_G^2 = 0.13$, nor between interval group and scene component $F(1, 28) = 2.39$, $p = 0.13$, $\eta_G^2 = 0.03$. In addition, there was no three-way interaction between interval group, category, and scene component $F(1, 35) = 2.18$, $p = 0.15$, $\eta_G^2 = 0.05$ indicating that, although there is an overall trade-off for positive scenes it does not differ between nap and wake groups (Figure 2S).

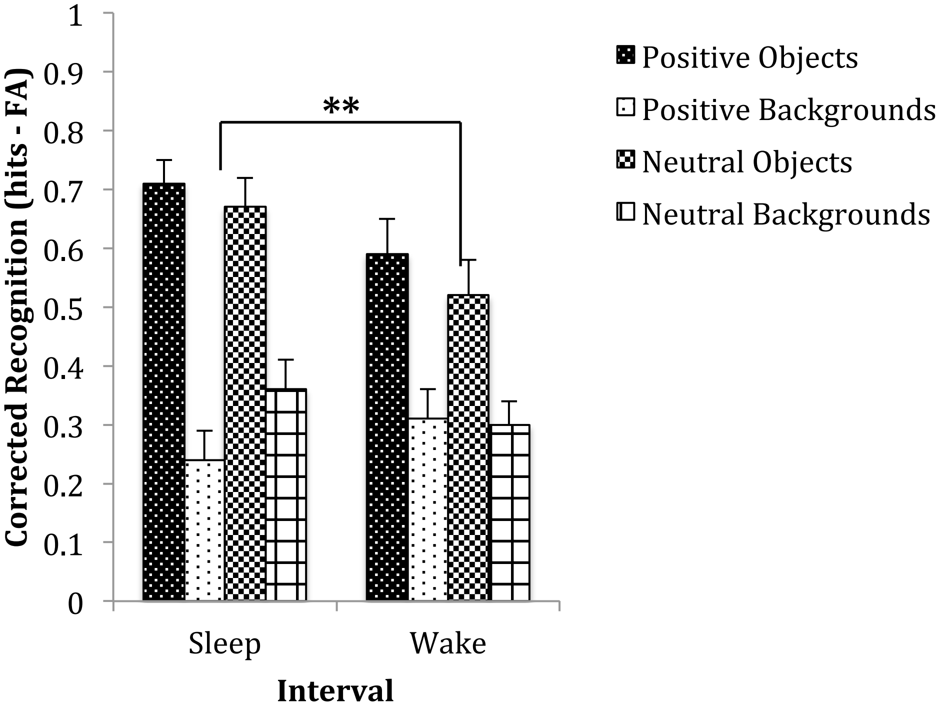


Figure 2S: Memory trade-off performance for high confidence responses for positive scenes for nap-interval and wake-interval conditions. $**p \leq 0.05$

Finally, for the distinctive category, there was not a significant main effect for interval group $F(1, 28) = 1.17$, $p = 0.29$, $\eta_G^2 = 0.04$, or for category $F(1, 28) = 0.35$, $p = 0.56$, $\eta_G^2 = 0.01$, but there was a significant main effect for scene component $F(1, 28) =$

53.01, $p < 0.005$, $\eta_G^2 = 0.65$. There was also a significant interaction between category and scene component $F(1, 28) = 11.09$, $p = 0.002$, $\eta_G^2 = 0.28$ and between interval group and category $F(1, 28) = 7.45$, $p = 0.01$, $\eta_G^2 = 0.21$. There were no significant interaction between interval group and scene component $F(1, 28) = 0.71$, $p = 0.41$, $\eta_G^2 = 0.01$. In addition, there was no three-way interaction between interval group, category, and scene component $F(1, 28) = 0.07$, $p = 0.80$, $\eta_G^2 = 0.00$. The results indicate that there was an overall difference in memory performance that does differ between nap and wake groups. However, this difference is not in the memory trade-off effect (Figure 3S).

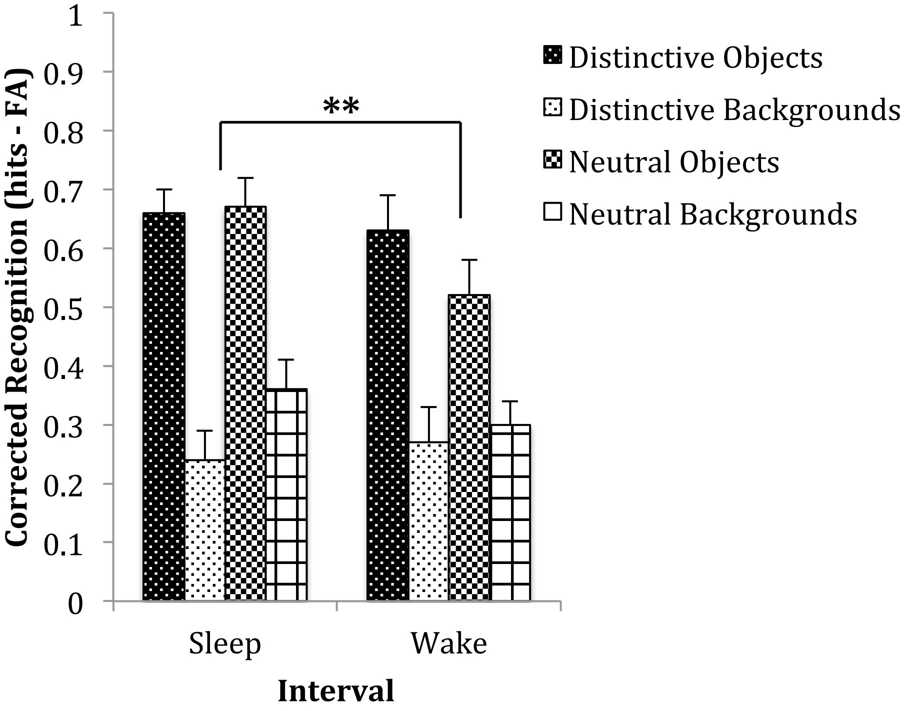


Figure 3S: Memory trade-off performance for high confidence responses for distinctive scenes for sleep-interval and wake-interval conditions. $^{**}p \leq 0.05$

Differences in the magnitude of the memory trade-off

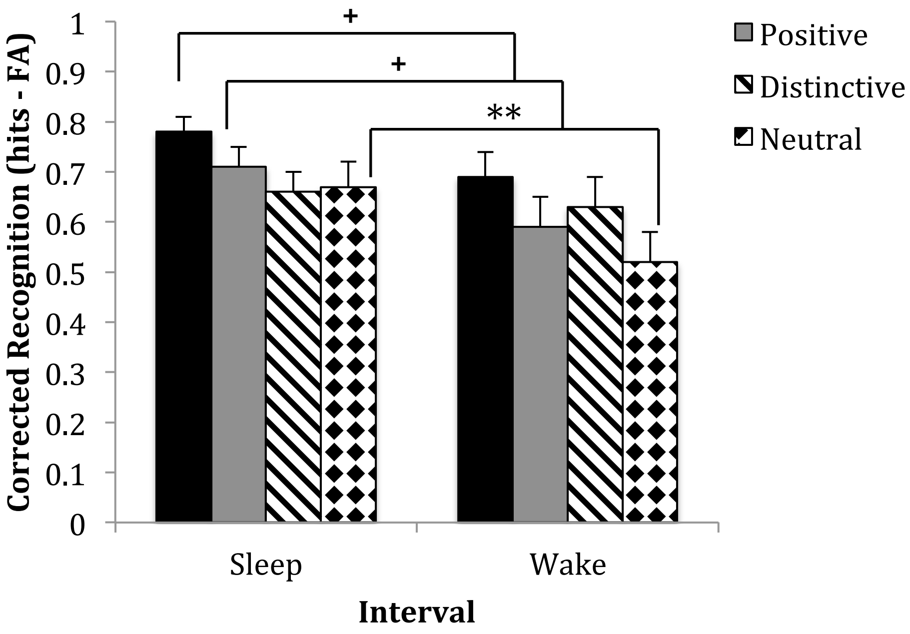
In order to determine whether there might be a difference in the magnitude of a memory trade-off for either emotional or distinctive scenes after an interval that included either sleep or wakefulness, repeated-measures ANOVAs were conducted using difference scores. A repeated-measures ANOVA with interval group (nap, wake) as the between-subjects factor and category (negative, positive, and distinctive) and scene component (item, background) as within-subjects factors did not result in a significant main effect for interval group $F(1, 28) = 0.25, p = 0.62, \eta_G^2 = 0.01$, for category $F(2, 56) = 2.57, p = 0.08, \eta_G^2 = 0.08$, although it might be marginal, or for scene component; $F(2, 56) = 0.17, p = 0.69, \eta_G^2 = 0.01$. There was a significant interaction between category and scene component $F(2, 56) = 3.72, p = 0.03, \eta_G^2 = 0.11$ suggesting there was an overall statistical difference in the magnitude of the memory trade-offs between emotional and distinctive conditions. However there were no significant interaction between interval and category; $F(2, 56) = 1.00, p = 0.38, \eta_G^2 = 0.03$, but there was a significant interaction between interval and component, $F(2, 56) = 5.27, p = 0.03, \eta_G^2 = 0.02$. There was no significant three-way interaction between interval, category, and component $F(2, 56) = 1.89, p = 0.16, \eta_G^2 = 0.06$, suggesting that there was no statistical different in the magnitude of memory differences between nap and wake interval groups.

Planned comparison independent t-tests examining interval conditions confirmed that there was no significant difference between interval conditions for magnitude of memory differences for negative items; $t(28) = -1.31, p = 0.20$, negative backgrounds; $t(28) = 0.63, p = 0.53$, positive items; $t(28) = -0.69, p = 0.50$, and distinctive backgrounds; $t(28) = 1.74, p = 0.09$. Difference scores for distinctive items was significantly higher in the wake interval group; $t(28) = -2.19, p = 0.04$, and higher for positive backgrounds in the nap interval group; $t(28) = 2.30$ $p = 0.03$. These results indicate that there are differences in the magnitude for memory trade-offs for distinctive items and positive backgrounds between nap and wake interval groups.

Other differences in memory performance between nap and wake groups

Due to the significant interaction between interval group and category in the omnibus ANOVA, which suggested that there were overall memory differences between nap and wake group for the different categories, repeated measures ANOVAs were conducted on items and backgrounds separately to further elucidate where the difference might be. In order to investigate the effect of a nap on memory for items in all categories a repeated measures ANOVA was conducted with interval group (nap vs. wake) as a between subjects factor and category (negative, positive, distinctive, and neutral) as a within subjects factor. There was no significant main effect for interval group; $F(1, 28) = 2.37$, $p = 0.14$, $\eta_G^2 = 0.08$, but there was a significant main effect of category; $F(1, 28) = 44.68$, $p < 0.005$, $\eta_G^2 = 0.27$. There was no significant interaction between interval and category; $F(1, 28) = 1.70$, $p = 0.20$, $\eta_G^2 = 0.07$, indicating that there was no overall difference in memory for items between groups but there was an overall difference in memory for items between categories, which did not differ between interval groups (Figure 5S-A). A repeated measures ANOVA was also conducted with the backgrounds with interval as a between subjects factor (nap, interval) and category as a within subjects factor (negative, positive, distinctive, and neutral). There was no main effect for interval group $F(1, 28) = 0.003$, $p = 0.96$, $\eta_G^2 = 0.00$, but there was a significant main effect for category $F(3, 84) = 2.80$, $p = 0.05$, $\eta_G^2 = 0.09$. There was no significant interaction between group and category $F(3, 84) = 1.89$, $p = 0.14$, $\eta_G^2 = 0.06$ indicating that there were differences in memory for backgrounds between categories but there were no differences between nap and wake interval groups (Figure 5S-B).

A


Negative
Positive
Distinctive
Neutral
+
+
**
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Corrected Recognition (hits - FA)
Sleep
Wake
Interval

B

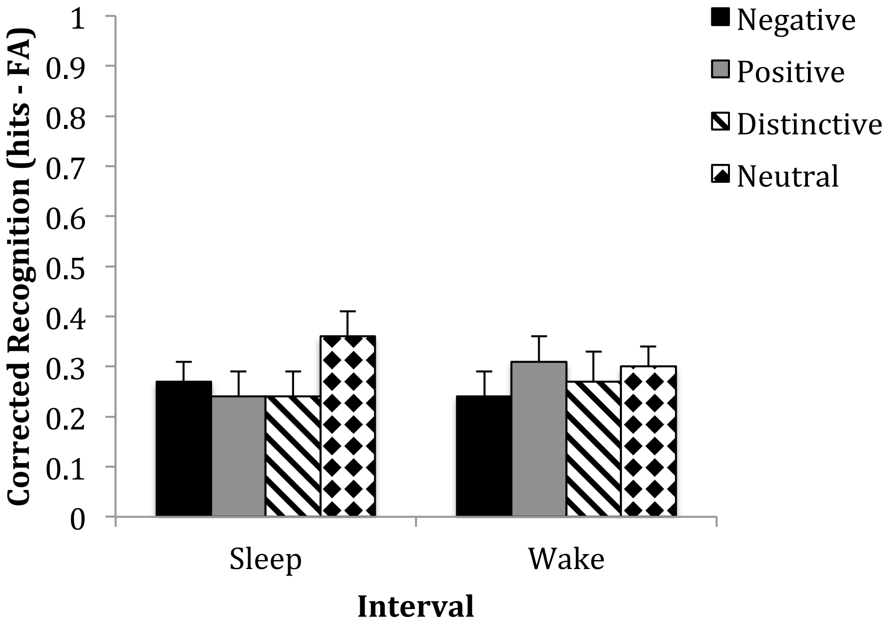

Negative
Positive
Distinctive
Neutral
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Corrected Recognition (hits - FA)
Sleep
Wake
Interval

Figure 4S: Corrected recognition performance for high confidence responses for sleep-interval and wake-interval conditions. A) Item Memory. B) Background Memory. $+p < 0.15$, $^{**}p \leq 0.05$

Planned-comparison planned independent t-tests confirmed that there was no difference in corrected recognition performance between nap-interval and wake-interval groups for negative items $t(24.84) = 1.57$, $p = 0.13$, positive items $t(28) = 1.55$, $p = 0.13$, and distinctive items $t(28) = 0.42$, $p = 0.68$. Memory for neutral items was significantly higher in the nap group compared to the wake group $t(28) = 2.08$, $p = 0.05$. There was no significant differences between nap and wake interval groups for backgrounds paired with negative items $t(28) = 0.45$, $p = 0.66$, backgrounds paired with positive items $t(28) = -0.97$, $p = 0.34$, backgrounds paired with distinctive items $t(28) = -0.47$, $p = 0.65$, and backgrounds paired with neutral objects $t(28) = 0.99$, $p = 0.33$.

General Discussion

Two experiments were conducted in the context of this thesis in order to explore the effects of sleep on preferential declarative memory consolidation for distinctive and emotional composite scenes. For both experiments, selectivity in memory was measured using a memory trade-off paradigm where composite scenes were created by superimposing a central item (either negatively arousing, positively arousing, visually distinctive but emotionally neutral, or neutral) on a neutral background. Participants studied each composite scene and then after an interval, 12-hours **(Study 1)** and 2 hours in **(Study 2) that** included either a period of sleep or an equivalent period of wakefulness, were tested on the different components of each scene separately to better measure what aspects of each scene were selectively remembered after the interval. The memory trade-off paradigm has previously been successful in demonstrating that both emotional and distinctive salient information attract visually attention at encoding and are selectively remembered over neutral information (Campanella & Hamann, in preparationa). In addition, it has been demonstrated that sleep selectively benefits emotionally salient information (Payne et al., 2008).

In the first experiment there was weak evidence for specific components of sleep mediating memory consolidation for neutral background information, although there was a lack of evidence for a behavioral benefit for sleep. Speculatively, the lack of a behavioral effect may be due to highly salient information (i.e., emotional and distinctive items) being equally well consolidated during sleep and wakefulness. With respect to background information, however, there was a weak selective sleep benefit for sleep duration. It has previously been demonstrated that there is a relation between the amount of sleep an individual gets and subsequent memory performance (for review, see Diekelmann et al., 2009). To be specific, the findings of Study 1 suggest that memory for background information (demonstrated with distinctive backgrounds) increases as individuals spend more time sleeping, or in a dose-dependent manner. However, relations between sleep duration and memory performance do not necessarily suggest active benefits of sleep on memory consolidation. Instead such findings can also suggest that memory improves over a period of time when there is no interference. As a result, in order to better measure the *active* benefits of sleep on memory consolidation it is necessary to examine the relation between memory performance for the different components and stages of sleep. Examining the relation between memory performance and specific physiological properties of sleep (i.e., sleep stages) was the focus of Study 2.

In the second experiment, the effect of different components of sleep on the memory trade-off was further explored using a 2-hour polysomnography-recorded nap. To be specific the effect of different stages and sleep spindles, which are a more fine-tuned physiological mechanism associated with Stage 2 sleep, on memory trade-offs was explored. In the second experiment, there were no differences in the magnitude of the trade-off between the nap group and wake group. There was, however, a marginal general enhancement in memory for all items. In addition, the enhancement for neutral items after a nap was significant. Moreover, there was evidence that different sleep stages: specifically Stage 2 and sleep spindles contribute to consolidate to different aspects of distinctive and neutral memory. Most importantly, the second experiment presented tentative evidence that emotional, distinctive, and neutral information are consolidated during sleep. In particular, there is behavioral evidence of sleep dependent consolidation for the neutral items and, to a lesser extent, the emotional items. In addition, there is correlational evidence of Stage 2 sleep influencing consolidation of positive items and background information. This illustrates the importance of examining different factors when examining the effects of emotion and saliency on memory consolidation. This last point, however, will need to be investigated further in future studies.

The following discussion section will address some of the emergent themes from these two studies. The goal of this discussion is two fold: first to examine how sleep might selectively consolidate memory, and second to address issues relevant to future research directions. More specifically the current results will be linked to previous theories of sleep actively consolidating memory. Finally, the idea that emotion or saliency may not always be the filter by which sleep selectively consolidates memory will be examined. This final point is consistent with the idea that in certain contexts sleep preferentially consolidates weakly encoded information (Drosopoulos et al., 2007; Kuriyama et al., 2004).

Sleep's Role In Selective Memory Consolidation Revisited

Increasingly it is becoming apparent that sleep plays an important and active role in memory consolidation. Although it was initially thought that the strongest benefits for sleep were for procedural memory (memory for skills) (Stickgold, 2005), emerging evidence suggests that sleep also consolidates declarative memory (memory for episodes and knowledge) (Diekelmann & Born, 2010; Ellenbogen et al., 2006). The role of sleep in memory consolidation is typically measured by comparing memory performance of learned information after an interval that includes either a period of sleep or equivalent period of wakefulness. Sleep is shown to increase memory performance (Diekelmann & Born, 2010; Ellenbogen et al., 2006; Gais & Born, 2004a; Maquet, 2001; Stickgold, 2005). It has also been demonstrated that in addition to strengthening memory sleep also increases resistance to interference (Ellenbogen et al., 2009, 2006). Furthermore, specific physiological properties may play different roles in the consolidation process (Fogel & Smith, 2006; Gais & Born, 2004b; Marshall et al., 2006; Mölle et al., 2002; Wagner et al., 2001). This suggests that sleep actively consolidates memory by either providing an ideal neurobiological environment for consolidation or through specific mechanisms during specific sleep stages (Diekelmann & Born, 2010; Diekelmann et al., 2009; Ellenbogen et al., 2006).

Increasing evidence, however, suggests that instead of globally enhancing memory performance sleep selectively consolidates information. To be more specific, evidence suggests sleep selectively consolidates highly salient information. Using intentional memory tasks, researchers have shown that sleep will selectively enhance rewarded information (Fischer & Born, 2009) and information deemed important for future relevance (Saletin et al., 2011; Wilhelm et al., 2011). Research also suggests that sleep will also selectively consolidate information, which is naturally salient, such as emotional information (Payne & Kensinger, 2011a; Payne et al., 2008). Using an incidental memory task, Payne et al (2008) showed participants negative and neutral composite scenes and tested recognition memory on the central and background components of each scenes. They demonstrated that sleep selectively consolidated memory for the emotionally arousing central components compared to neutral central components and backgrounds paired with negative and neutral items, otherwise known as a memory trade-off.

A prominent theory for why emotional information may be preferentially consolidated during sleep is that emotional arousal determines saliency. As a result, emotionally salient central aspects of an episode are preferentially encoded at the expense of neutral and background information. This preferential encoding will, in turn, lead to selective consolidation during sleep (Payne & Kensinger, 2010). This view, however, neglects the role that other factors such as valence and distinctiveness have on filtering (or "tagging" as it is referred to in the literature) information for selective consolidation. It is possible that valence and distinctiveness can also preferentially direct attention at encoding, thus resulting in stronger encoding and preferential consolidating. The current group of studies investigating this question did not see an enhanced memory trade-off after a period of sleep, and therefore did not support the previous literature. Instead, in **Study 1** there was no behavioral difference in memory performance between sleep and wake interval groups, whereas **Study 2** showed a benefit neutral items, which are not typically considered salient. There was also a marginal benefit to negative items though not as pronounced as with neutral items. Although these findings do not match previous findings mentioned above they do support evidence that sleep may, under certain conditions, also consolidate lower valued information (Oudiette et al., 2013) or more weakly encoded information (Drosopoulos et al., 2007; Kuriyama et al., 2004). The current findings may also support evidence that sleep may not always preferentially consolidate emotional information (Baran et al., 2012; Lewis et al., 2011), and that neutral information may also be sensitive to sleep benefits (Atienza & Cantero, 2008).

As a result of these conflicting findings, it remains necessary to determine how memories are ultimately selected for consolidation during sleep. The logic behind the theory that salient information is preferentially consolidated is that strongly encoded information will ultimately be consolidated during sleep. However, a recent study demonstrated that when participants were instructed to remember items, which had been assigned a point value on a 1-20 scale and obtain the highest points possible, sleep did not preferentially benefit memory for high value items. Instead, sleep enhanced overall memory for both low and high value items but did not do so as a function of increasing relevance (Baran et al., 2013). Thus, although most studies agree that there seems to be some sort of filter in place for what type of information will ultimately be consolidated, there are limitations and the filter may ultimately not be memories which are most strongly encoded. In fact, it has been demonstrated that most highly rewarded information, which would likely be more strongly encoded than low reward information, may be equally well consolidated during wakefulness and sleep (Dupret et al., 2010; Oudiette et al., 2013; Singer & Frank, 2009).

Ultimately it may be an issue of the context under which information is learned. In the case of previous studies investigating emotion-induced memory trade-offs or comparing memory for emotional and neutral information negative stimuli is compared to neutral, making the distinction between relevant and non-relevant information simple. In the current set of experiments, on the other hand, there are 4 different categories (negative, positive, distinctive but emotionally neutral, and neutral), which may have complicated the issue of relevancy and ultimately what is consolidated during sleep. It is possible that overall the central thematic items (all the items in the current study) were judged as relevant information. All presented items would therefore be more susceptible to consolidation during sleep (seen in **Study 2**) under some generalizable rule, such as being objects superimposed on a background. Evidence, which supports the above theory, has demonstrated that sleep promotes processes of generalization and abstraction (Gómez et al., 2006; Lau et al., 2011; Wagner et al., 2004), which in turn may explain how memories are consolidated during sleep. Similar evidence is seen using the Deese-Roediger-McDermott paradigm which involves participants learning word lists of semantically related words and then being tested on those words and semantically related lures (Roediger & McDermott, 1995). It has been shown that participants are more likely to generalize the semantic gist of word lists after sleeping (Payne et al., 2009). By contrast, in previous trade-off studies (Payne et al, 2008) the comparison between negative and neutral may have highlighted only the negative central items.

It is also important to note that the results of **Study 1** are not really discussed in this section as it is unclear how sleep is selectively consolidating information due to the lack of difference in memory performance between groups.

Mechanism By Which Sleep Consolidates Memory

Most of the behavioral evidence for a selective memory benefit after sleep comes from **Study 2**. However, both experiments demonstrate that physiological components of sleep weakly correlate with memory performance suggesting that sleep may actively consolidate memory. The predominant theory, is that memories are reactivated during sleep, and more specifically during SWS (though also Stage 2 sleep, another nonREM sleep stage) (Diekelmann et al., 2012; Peigneux et al., 2004; Wilson & McNaughton, 1994). Reactivation during sleep is thought to reflect systems consolidation processes during memories are redistributed and re-organized in existing knowledge networks (Diekelmann & Born, 2010). Emotional processing or consolidation of more implicit information, on the other hand, occurs during REM sleep (van der Helm et al., 2011; Wagner et al., 2001; Walker & van Der Helm, 2009). An alternate theory, termed *synaptic homeostasis hypothesis*, posits that during sleep the brain undergoes global synaptic downscaling, where only strong synaptic connections are retained after sleep. As a result of this downscaling, information which was strongly encoded will be selectively remembered after sleep (Tononi & Cirelli, 2003, 2006). Both theories may explain why high salient information is typically preferentially consolidated during sleep. However, evidence from the current set of studies supports the view that sleep is actively consolidating memory as the strongest benefits of sleep were seen for neutral information, which is traditionally thought to be more weakly encoded than emotionally salient or distinctive information. This finding cannot be explained by synaptic homeostasis but can be explained by active consolidation theories.

With respect to how memories might be actively consolidating during sleep, there are two possible explanations. One theory posits that sleep stages play different roles in memory consolidation. More specifically, that NREM stages of sleep—with strongest evidence supporting SWS sleep and increasing evidence implicating Stage 2 sleep and specifically sleep spindles—are involved in the reactivation of declarative information which ultimately leads to enhanced memory (Diekelmann & Born, 2010; Wilson & McNaughton, 1994). Emotional processing, on the other hand, occurs during REM sleep (Nishida et al., 2009; Walker & van Der Helm, 2009). Alternatively, sleep benefits may be strongest as a result of the sequence of SWS followed by REM sleep, as explained by the *sequential hypothesis* (Ambrosini & Giuditta, 2001; Giuditta et al., 1995). Specifically, SWS reflects systems consolidation processes where, newly encoded memories are redistributed from the hippocampus to the neocortex and re-organized in existing knowledge networks. The succeeding REM sleep periods then reflect times when synaptic consolidation processes are at work and redistributed and reorganized memories are further strengthened and stabilized. Under this view, the greatest sleep benefits will be seen after a sleep period, which includes periods of SWS followed by periods of REM. Stage 2 sleep is thought to also be involved in the initial re-organization and redistribution process (for discussion, see Diekelmann & Born, 2010). The current group of studies cannot definitely support one view over the other. In Study 2, Stage 2 sleep (and sleep spindles) seemed to primarily benefit memory for neutral backgrounds and positive items, which could fit both theories. However the lack of a benefit for memory after REM sleep makes it difficult to distinguish between the theories. Along this same vein, previous evidence has demonstrated that SWS (also NREM sleep but with different physiological correlates) and REM may have complementary roles in enhancing emotional information (Cairney et al., 2014). However, it is difficult to conclude how much the current studies fit into this model, as Stage 2 sleep was not specifically addressed in the Cairney et al. (2014) study. It is also important to note that in Study 2, not all participants reached SWS sleep, and indeed, some participants skipped SWS during the nap and progressed from Stage 2 sleep directly to REM. In addition not all participants reached REM sleep, or even experienced a substantial period of sleep. It would interested to see whether behavioral benefits would have been stronger in the nap group had all participants experienced a nap with both SWS and REM periods. Further experimentation, therefore, is necessary to better determine the mechanisms by which sleep consolidates memory.

Future Directions

The current set of studies was enlightening in that they provided evidence for sleep actively consolidating memory. More interestingly, the two studies presented evidence that suggests that sleep may not always preferentially consolidate information which would be considered highly relevant. However, many questions still remain as to how these memories are consolidated. In this section, I address possible ways to begin to answer lingering questions.

Of note in Study 2 was the benefit in memory for neutral information associated with sleep. Currently it is somewhat difficult to determine whether sleep always benefits neutral information, as other studies have not observed this phenomenon (Payne et al, 2008; Wagner et al, 2001). In addition, it is unclear if the lack of a magnified memory trade-off effect is a result of differences in the memory trade-off paradigm utilized by Payne et al, (2008). As it was previously mentioned, the addition of two categories (positive and distinctiveness) may have caused participants to generalize all the objects during sleep, thus resulting in the marginal benefit of sleep for all objects and significant increase for neutral objects. In order to better determine whether distinctive information undergoes similar consolidation processes to negative information, it would be interesting to compare just distinctive scenes to neutral and see whether behavioral performance compares to what was seen in previous studies comparing negative scenes to neutral (Payne et al., 2008). Similar comparisons could also be made with positive scenes and neutral to see whether there are differences in how valenced information is consolidated.

In addition, in the current studies it is unclear whether reactivation is the specific mechanism by which memories are selectively consolidated during sleep. Thus it would be interesting to use a targeted-reactivation paradigm similar to that employed by (Oudiette et al., 2013; Rasch et al., 2007; Rudoy et al., 2009), during which emotional, distinctive, and neutral items are paired with cues (either odor or sound cues), which are then re-presented during either periods of sleep (SWS and REM to see the effects of each sleep stage) and wakefulness. This paradigm—during which reactivation is directly manipulated by representing cues during offline periods—could help determine how memories are reactivated during sleep. Moreover, it would better address the hypothesis proposed in Study 1 that highly salient information (defined as emotional and distinctive information in the current study) may equally well consolidated during periods of quiet wakefulness, whereas neutral information may be selectively consolidated during sleep.

Finally, one of the weaknesses of the current paradigms is that the measures of sleep stage may not be sensitive enough to detect the function of different sleep features in memory consolidation. Sleep staging can be somewhat of a crude measurement where the impact of specific physiological components on cognition may be lost. The field is beginning to address this limitation by examining specific components: such as sleep spindles (stage 2 and SWS; (Dijk, 1995; Fogel & Smith, 2006; Saletin et al., 2011), delta rhythms (Marshall et al., 2006), neurochemical changes during sleep (Bennion et al., 2013; Born & Wagner, 2004; Gais & Born, 2004b), and theta activity (Nishida et al., 2009). Thus it may be necessary to include additional analyses where some of these features are also examined. In Study 2, there was a weak relation between sleep spindles and memory performance, which suggests that it may be fruitful and informative to include these additional more fine-tuned analyses moving forward.

Concluding remarks

The question of how sleep preferentially consolidates some memories over others is a question that has been of great interest to sleep and cognitive scientists for years. Evidence suggests that highly salient information will primarily benefit from post-encoding sleep, by using paradigms where salience was manipulated by the experimenter (i.e., assigning relevancy or reward), or using emotional stimuli, which could be considered natural salient. A common feature of the previous studies is that sleep consolidates information, which, presumably, is encoded more strongly. The current group of experiments examined what specific properties of emotion (i.e., arousal, valence, and distinctiveness) may mediate selective consolidation during sleep. Although there was evidence that sleep plays an active role in consolidating memory, the benefit was primarily observed for neutral information. The results of the current two studies do not support previous literature showing only a selective benefit for emotional information. The results do, however, match findings from previous studies that have also found sleep benefits for neutral information. What this suggests is that under certain contexts, in the presence of emotional or salient information, sleep may also consolidate weakly encoded information. The findings of the current study also illustrate the need to examine which encoding factors may act to filter certain memories for selective consolidation during sleep.

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