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Examining the effects of post-learning sleep on consolidation of emotional declarative memories

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SLEEP AND EMOTIONAL MEMORY CONSOLIDATION

Examining the effects of post-learning sleep on consolidation of emotional declarative memories

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B.S., Purdue University, 2005

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Abstract

Examining the effects of post-learning sleep on consolidation of emotional declarative memories

By Carolina Campanella

Considerable research suggests that sleep can enhance the consolidation. Notably, the enhancing effects of emotion on memory have also been linked to enhanced memory consolidation, and specifically to hippocampal-dependent consolidation processes proposed to occur during sleep. However, this has only been investigated for negatively arousing memories and the effects of valence is currently unknown. An additional essential feature of declarative memories is the ability to bind different attributes of an event together and maintain these associations. Previous studies suggest sleep plays a key role in strengthening these associations, and this facilitation may be greater for emotionally salient stimuli than for emotionally neutral stimuli. However, it remains unclear whether post-learning sleep preferentially boosts emotional associations relative to neutral associations, in a similar way that it boosts memory for emotionally arousing single items. Using recognition and cued recall memory tasks, we examined whether sleep preferentially enhanced memory for positive and negative pictures (item memory) and negatively arousing verbal paired associates (associate memory) over neutral pictures and word pairs. Participants studied both emotional (positive and negative) and neutral pictures, and emotional (negative) and neutral verbal paired associates. Following a 12-hour break filled with either a period of sleep or wakefulness, participants were given surprise cued-recall (for the word pairs) and a recognition tasks (for the pictures). As prominent theories suggest that emotion enhances event memory during consolidation, via the modulatory effect of the amygdala on medial temporal lobe regions, retrieval of emotional items (relative to neutral ones) was expected to be preferentially enhanced after post-learning sleep. Results indicated that post-learning sleep did not enhance recognition memory performance, possibly due to ceiling effects in memory performance. Our results for cued-recall performance confirmed established literature that sleep enhances associative memory. However, the effect of sleep was equivalent for negative and neutral pairs, rather than disproportionately enhancing memory for negative pairs. Our results suggest the enhancing effect of sleep on paired-associate cued recall is independent of the emotional arousal of target items. These results contrast with previous findings and indicate the effects of sleep on memory for emotional material can differ substantially across different memory tasks.

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The benefits of sleep on memory have been noted since the first century AD, when Quintilian, a Roman philosopher, stated that "what could not be repeated at first is readily put together on the following day; and the very time which is generally thought to cause forgetfulness is found to strengthen the memory" (Honeycutt, 2006, ¶ 16). Subsequent scientific study has revealed that sleep plays multiple roles in influencing memory. Initial studies of the effect of sleep on memory focused on its role in enhancing procedural memory, a form of memory involved in perceptual and motor learning. These studies found that sleep plays a modulatory role in procedural memory by enhancing the stabilization or consolidation of new procedural learning (reviewed in Stickgold, 2005; Peigneux, Laureys, Delbeuck & Maquet, 2001; Gais, Philal, Wagner & Born, 2000). Sleep following learning has a significant beneficial effect on several forms of procedural learning, including learning new motor sequences (Walker, Brakefield, Morgan, Hobson & Stickgold, 2002), perceptual learning of auditory discrimination for synthetic language stimuli (Fenn, Nusbaum & Margoliash, 2003), and learning in serial-reaction-time tasks (Peigneux et al, 2003).

Following on these initial findings in procedural memory, more recent research has now begun to investigate the effect of sleep on declarative memory, defined as memory for facts and events that can be accessed consciously (Gais, Lucas & Born, 2006; Ellenbogen, Hulbert, Stickgold, Dinges, & Thompson-Schill, 2006a). A growing number of studies have found that post-encoding sleep (i.e., sleep occurring shortly after a learning episode) can enhance declarative memory (for review, see Ellenbogen, Payne

& Stickgold, 2006b). However, post-encoding sleep has sometimes been found not to enhance memory (Vertes, 2004), and, as yet, relatively few studies have addressed the role of sleep in declarative memory. Thus, currently, there are significant gaps in understanding of the nature of sleep's effects on declarative memory as well as its underlying neurobiological mechanisms.

The effects of sleep on memory can be usefully distinguished based on the stage of memory processing targeted by the experimental sleep manipulation. Memory processing is conventionally divided into three stages: encoding (the initial formation of a memory representation), storage and consolidation (processes related to the retention of memory representations over a delay, including dynamic processes whereby memories are converted into more stable and enduring forms), and retrieval (processes involved in retrieving and reconstructing aspects of the encoded memory representation). Although studies have examined the effect of sleep on each of these three stages of memory processing, particular interest has focused on the effects of sleep on memory consolidation (reviewed in Walker & Stickgold, 2006). Consolidation is a hypothesized process that converts initially labile and fragile memory representations into a more enduring form, thereby facilitating the long-term retention of memories over intervals of weeks or years (Dudai, 2004). Consolidated memories are hypothesized to not only be more enduring than unconsolidated memories, but also are proposed to be differ qualitatively from them. For example, consolidated memories are proposed to be more resistant to several influences that tend to produce forgetting, including interference processes (McGaugh, 2000; Robertson, Pascual-Leone & Press, 2004). Although a growing body of research suggests that sleep enhances declarative memory consolidation, as noted previously, studies have only just begun to investigate the nature of the ways in which sleep affects consolidation of declarative memory (Ellenbogen et al, 2006b).

Contemporary Theories on Sleep and its Effects on Declarative Memory Consolidation

Ellenbogen et al (2006b) recently summarized four current leading theories of the proposed effects of sleep on declarative memory consolidation. The first of these theories proposes that sleep has no effect on declarative memory consolidation. By this view, enhancement of memory performance overnight after learning results from the passage of time rather than any special function of sleep (Vertes, 2004). This theory has been challenged by empirical evidence from several studies demonstrating enhanced declarative memory performance in individuals who slept immediately after learning, relative to individuals who remained awake for an equivalent delay (Ellenbogen et al, 2006a; Gais & Born, 2004; Hu, Stylos-Allan & Walker, 2006; Payne, Stickgold, Swanberg & Kensinger, 2008). While it is widely believed that certain types of consolidation occur during waking periods (Ellenbogen et al, 2006b), the enhanced memory performance observed after sleep suggests that post-learning sleep can have specific enhancing effects on declarative memory. Thus, as Ellenbogen et al. conclude, this theory that sleep does not affect memory consolidation is generally regarded as lacking in empirical support.

A second theory, and one of the oldest, proposes that post-learning sleep enhances memory by temporarily protecting declarative memories from the deleterious effects of interference, but that sleep plays no role in consolidation (Ellenbogen et al, 2006b; Wixted, 2004; Jenkins & Dallenbach, 1924). This view is motivated in part by findings from numerous studies that have demonstrated that, following a given learning episode, cognitive activity and additional learning can interfere with the subsequent retrieval of the initially learned material, a phenomenon termed retroactive interference (Wixted, 2005). If more cognitive activity occurs during periods of wakefulness than during periods of sleep (of the same duration), then this additional cognitive activity could potentially increase the amount of retroactive interference and thus impair subsequent memory for the initially encoded material. In other words, this view proposes that sleep plays a passive role by providing a temporary protection or shelter from the negative influence of interference from waking life, but sleep has no role in altering consolidation processes or otherwise changes the nature of memory representations. By this view, one would expect that memory for material learned just prior a night's sleep would be superior to memory for the same material when learning was followed by an equal delayed filled with wakefulness.

Recent studies looking at verbal recall, interference and sleep seem to disagree with the idea that sleep's role in memory is passive. Gais, Lucas and Born (2006) found that sleep following learning improved recall for words in adolescents and that this improvement in recall was independent of the amount of time awake after the sleep period, suggesting that memories had been consolidated during the sleep period. In another study, Ellenbogen et al (2006a) found that sleep provided protection against the negative effects of experimental manipulations of interference on memory, and critically, that sleep protected studied verbal material from future interference. The fact that material studied prior to sleep continued to be resistant to the effects of experimental interference is inconsistent with a passive, temporary protection role for sleep, and is more consistent with the view that sleep enhances consolidation. The view that sleep enhances consolidation has two related versions, which differ mainly in whether special neurobiological mechanisms are proposed to enhance consolidation during sleep.

In one version (theory three), sleep enhances consolidation *indirectly* by reducing factors, primarily interference, thereby allowing consolidation to proceed unfettered by waking cognitive activity. By this view, sleep creates conditions that are ideal that for consolidation but plays no other special or distinctive role in the process. Similar to the passive-sleep-role theory described earlier (theory 2), this hypothesis assumes that sleep protects memories from interference. However, unlike the earlier sleep theory, this particular hypothesis states that the reduced interference during sleep facilitates consolidation (Ellenbogen et al, 2006b). Essentially, by reducing interference, sleep allows the existing consolidation to function more efficiently.

The final theory (theory four), proposes that special physiological properties of sleep are *directly* involved in enhancing declarative memory consolidation (Ellenbogen et al, 2006b). Recent studies have begun to address the idea that specific components of sleep's physiology lead to memory consolidation and a variety of neurobiological mechanisms for enhanced sleep-dependent memory consolidation have been proposed. One of the leading models proposes that consolidation of declarative memories occurs primarily during sleep stages 1-4 or non-REM sleep (NREM) (Gais & Born, 2004; Plihal & Born, 1997; Rauchs, Desgranges, Foret & Eustache, 2005). Several studies have reported superior memory recall among participants who slept during the first part of the night, which contains relatively more slow wave sleep (SWS) than sleep later in the night, compared to those who were awake for the same time period (Gais & Born, 2004).

More importantly, this effect was not seen in participants who slept during the second half of the night, when relatively less SWS occurs.

Intracellular in vivo studies studying 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 animal studies have demonstrated that recently acquired hippocampus-based memories are 'replayed' during sleep (Wilson & McNaughton, 1994; O'Neill, Senior & Csicsvari, 2006). Studies looking at recently acquired memories for spatial navigation found that replay occurred in the hippocampus both during periods of wakefulness and sleep. During wakefulness, memories would be replayed backward (Foster & Wilson, 2006) whereas during sleep would replay forward (Suzuki, 2006) suggesting different processes. Specifically, that initial learning relies on reverse replay whereas consolidation occurs during forward replay (Ellenbogen et al, 2006b). Neuroimaging findings in humans lend support to the idea that hippocampus-dependent memories are reactivated during sleep by demonstrating that increased hippocampal activity during sleep following spatial learning leads to behavioral improvement during recall (Peigneux et al, 2004).

An alternative sleep-dependent active memory consolidation view maintains that all stages of sleep are important for declarative memory consolidation by underscoring the idea that each stage of sleep occurs in succession several times throughout the night. Therefore it is possible that the interplay of sleep stages within an ultradian cycle, which repeats several times throughout the night, coordinates different feed-forward and feed-back mechanisms between the hippocampus and neocortex that enhance memory consolidation (Ellenbogen et al, 2006b). Ficca, Lombardo, Rossi and Salzarulo, 2000 found that disrupting the ultradian cycle led to impaired recall of verbal material the next morning, suggesting that both NREM and REM sleep are essential for declarative memory consolidation.

The current study, which was motivated by the idea that sleep modulates declarative memory consolidation either indirectly (theory 3) or directly (theory 4), investigated the effects of sleep on declarative memory consolidation across the entire night. Therefore, the current study was unable to address any specific questions regarding the neurobiological mechanisms that may occur during sleep-dependent memory consolidation.

Emotion and its Effects on Declarative Memory Consolidation

An important factor influencing memory consolidation is the emotional strength or arousal associated with the material being learned (Phelps, 2004). Additionally, arousal ensures that emotional memories endure more strongly over time than neutral memories (McGaugh, 2004). Moreover, emotionally arousing stimuli can even enhance memory of other previously presented neutral stimuli (Anderson, Wais & Gabrieli, 2006). Emotional arousal is thought to influence memory consolidation in part via upregulation of hippocampal activity via outputs from the amygdala, a structure whose activity is often increased during the processing of emotionally arousing stimuli (McGaugh, 2004). Several studies have demonstrated that the amygdala selectively contributes to the enhancement of emotional but not neutral declarative memories (Cahill, Babinsky, Markowitsch & McGaugh, 1995; Cahill et al, 1996; Hamann, Ely, Grafton & Kilts, 1999). Additionally, it has been suggested that these beneficial effects are modulated by neurohormonal and neuromodulator changes (McGaugh, 2004).

Converging evidence suggests that consolidation occurs in the medial-temporal lobe (MTL) memory system (Rugg & Yonelinas, 2003; Yonelinas, Otten, Shaw & Rugg, 2005). An influential view of the function of this memory system proposes that the hippocampus is specifically involved in the processing of memory representations that support *recollection*, in which the original episode and aspects of its context (e.g. thoughts, feelings and sensory details that "take you back" to the original episode) are retrieved, whereas other structures such as the perirhinal cortex (PRC) mediates *familiarity*, where an item can be discerned as having occurred before, but without recollection of its context (Yonelinas, 2002; LaBar & Cabeza, 2006). Combining the view that emotion influences memory primarily via amygdala effects on the hippocampus, and the proposed specific hippocampal role in recollection, one would predict that emotion would affect recollection over familiarity. Indeed, several studies bear out this prediction, finding that emotional arousal during encoding enhances subsequent recollection but not familiarity components of recognition (Sharot & Yonelinas, 2008).

Effects of Sleep and Emotion on Memory Consolidation May Interact

Memory consolidation is thought to be a slow process, lasting hours, weeks, months, or even years (Dudai, 2004). Likewise, the enhancing effects of emotion on declarative memory performance are often magnified after longer (≥24 hr) retention delays (Sharot & Yonelinas, 2008). This time-dependent effect of emotion is consistent with the possibility that emotion may influence slow, offline memory-consolidation processes after learning, possibly during sleep. Recent studies have also examined the impact of a full night of sleep on memory of neutral and negatively emotional items and found an enhancement in retention of negative material across periods containing sleep compared to equivalent time periods awake (Hu et al, 2006; Payne et al, 2008). Hu et al, (2006) compared offline consolidation of emotionally negative arousing and non-arousing neutral picture-stimuli following a 12 hour period across the day or across an equivalent period at night containing sleep. Participants in the sleep and wake groups showed no significant difference in memory for neutral items whereas the sleep group showed significantly improved memory performance for the emotional items. Interestingly, the greatest facilitation in memory was observed for pictures deemed to be familiar but not fully recalled suggesting that sleep enhances more general 'gist' type memory.

This result directly contradicts with previous evidence that maintains that only recollection memory benefits from emotion (Ochsner, 2000; Sharot, Verfaellie & Yonelinas, 2007) and from a short retention interval of sleep[1] (Drosopoulos, Wagner, & Born, 2005; Rauchs et al, 2004). Although it is possible that that sleep and emotion interacted to enhance memory based on the subjective experience of knowing, it remains unclear why recollection judgments were not enhanced for emotional and/or neutral items after sleep as one would predict, warranting further investigation. Additionally, Hu et al, (2006) did not fully control for circadian effects, which could be influential as participants underwent encoding and testing at different times of day. Circadian influence on encoding has been demonstrated to be critical for later memory recognition (Canli, Zhao, Brewer, Gabrieli & Cahill, 2000; Dolcos, LaBar & Cabeza, 2004).

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[1] Effects of emotion were not tested in these two studies.

Therefore, one explanation could be that circadian influences affected encoding subsequently leading to more conservative judgments during the testing period. More recently, it has been shown that sleep will preferentially consolidate emotionally negative objects embedded within a neutral scene, rather than the image as a whole (Payne et al, 2008).

Most studies to date have focused on the effects of negative emotional arousal on emotional memory, including studies of the effects of emotion on sleep and consolidation (Wagner, Gais & Born, 2001; Hu et al, 2006; Payne et al, 2008). Interestingly, no study has yet examined whether sleep has a role in consolidating positive emotional memories after learning. The role of sleep on positive emotional memories cannot be simply extrapolated from current knowledge about negative memories, particularly given evidence that positive and negative memories differ in several important respects including the relative role emotion in enhancing recollection and familiarity (Kensinger, 2004; Ochsner, 2000).

Previous findings suggest that recollection could be preferentially enhanced for negative information, relative to positive for various reasons. First, attentional and perceptual biases (e.g. threat, weapons focus) are commonly found for negative but not for positive stimuli, leading in a narrowing of attention for the most salient (i.e. negative) items in a scene (Christianson & Fallman, 1990). Second, people have the tendency to ruminate about and more extensively elaborate about negative information (Thomas & Diener, 1989). Finally, it seems more adaptive for organisms to have mechanisms in place to allow them to be able to quickly detect and strongly recollect negative and survival relevant material (reviewed in Ochsner, 2000).

To date, consolidation of positive emotional memories has only been studied in the context of sleep deprivation rather than manipulation of post-learning sleep (Atienza & Cantero, 2008; Sterpenich et al, 2007). However, memory impairment resulting from sleep deprivation can be explained by increased stress due to prolonged wakefulness, rather than lack of sleep, and could introduce other confounding factors. Atienza and Cantero (2008) compared remember (index of recollection) and know (index of familiarity) judgments for emotional and non-emotional images after a night of post-learning sleep or sleep deprivation. Their results indicated that sleep deprivation resulted in impairment of accuracy at retrieval of positive and neutral images. However sleep deprivation did not significantly reduce recollection accuracy of negative images and familiarity was unaffected by emotion or sleep, indicating that emotion and sleep may differentially influence the subjective experience of recollection and familiarity.

Rather than measure impairments in emotional memory performance as a result of sleep deprivation, the current study investigated the benefits of normal post-learning sleep for recollection and familiarity of emotional and non-emotional items, thereby reducing any confounding variables related to stress of prolonged wakefulness.

The first aim of this study was to determine the extent to which a period of post-learning sleep enhances recollection vs. familiarity processes in declarative memory. Using remember/familiar/new paradigm, we compared memory performance for neutral and emotional images and verbal paired-associates after a 12 hour retention interval during which participants either engaged in a full night's sleep or remained awake. Based on the results of several studies of the effects of post-learning sleep on subsequent recognition memory (Ellenbogen et al, 2006a; Gais et al, 2006; Payne et al, 2008), each of which found that post-learning sleep enhanced recognition memory, we predicted that recognition memory performance in the sleep group would be enhanced compared to the waking control group. The question of primary interest for this aim was whether post-learning sleep differentially affected the recollection (indexed by correct "remember" responses) and familiarity (indexed by correct "familiar" responses) components of recognition. We expected that post-learning sleep would enhance recollection to a greater degree than familiarity, based on prior evidence that maintains that only recollection benefits from a retention interval of sleep (Drosopoulos et al, 2005; Rauchs et al, 2004).

The second aim of this study was to examine whether the effects post-learning sleep on declarative memory differ for positive vs. negative emotional memories. The strength of emotional arousal experienced during encoding of emotionally arousing stimuli is typically the most important determinant of the degree to which emotion will enhance subsequent memory performance, independent of the positive (pleasant) or negative (unpleasant) emotional valence of the stimulus (McGaugh, 2004; Phelps, 2004). For example, several studies have demonstrated than when emotional arousal is equated between positive and negative pictures, words, and other stimuli, subsequent memory performance is enhanced to an equivalent degree.

To date, an unexplored question has been whether post-encoding sleep influences the emotional enhancement effect on declarative memory differently as a function of whether the emotional stimuli are positive vs. negative. As noted previously, post-encoding sleep itself enhances declarative memory. One possibility is that the effects of post-encoding sleep and emotion on memory act independently and combine to have additive effects. Alternately, processes occurring during post-encoding sleep, such as consolidation, may interact with emotional valence and affect memory for positive and negative stimuli differently. Moreover, valence-specific effects of post-encoding sleep may also be manifested differentially for the recollection vs. familiarity components of recognition. By this view, post-encoding sleep should increase recollection of negative items due to deeper encoding, which results in more salient and contextual details (e.g. thoughts or feelings) associated with the original episode being consolidated and later recalled. In contrast, post-encoding sleep should increase familiarity of positive items and not recollection as fewer contextual details are recalled in this scenario (Kensinger, 2004). Nevertheless, previous studies suggest that the degree of arousal and not valence will modulate memory consolidation (for review see McGaugh, 2004) and this effect will be seen after post-encoding sleep (Atienza & Cantero, 2008). In the current study we tested both predictions and hypothesized that the enhancement of memory after post-learning sleep would be highest for negative items, relative to positive and neutral items

Methods

Participants

Sixty-five students from Emory University participated for payment or class credit. Twenty-three participants were excluded from the final analysis for various reasons; eleven participants withdrew after the first session[2], seven participants were excluded because they did not meet the criteria for the study[3], and five participants were excluded for bad data[4]. The final data set included forty-two students from Emory University (mean age= 21.48 years, *SD*= 3.13). They were pseudo-randomly assigned to one of four conditions: sleep-12 hour-delay condition (N=12, 8 females), wake-12 hour-

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[2] Ten of these participants were in the sleep-delay group and one participant was in the wake-delay group

[3] Epworth score >10

[4] False alarm rates above chance

delay condition (N=12, 8 females), morning 30 min condition (N=9, 5 females) and an evening 30 min condition (N=9, 3 females). Participants who were in the sleep-delay condition viewed the stimuli at 9 pm and were tested 12 hours later, at 9 am the following morning, after a full night (7-8 hours) of sleep. Participants who were in the wake-delay group viewed the stimuli at 9 am in the morning and were tested 12 hours later, at 9 pm. Additionally, participants in the wake-delay condition did not nap during the 12 hour delay. The two circadian control groups viewed the stimuli at 9 am (morning 30 min condition) or 9 pm (evening 30 min condition) and were tested 30 min later (Figure 1, for 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, or pathological sleepiness (defined by an Epworth Sleepiness Scale score > 10) were excluded from participating. Furthermore, participants were asked to keep a sleep log during the week prior to the first session. On average participants slept an average of 7.9 hours per night (*SD*=1.1).

Materials

Both visual and verbal stimuli were used for this study to test item recognition and associative cued recall. For the set of pictures, which were used to look at item recognition, 360 affective pictures were selected from the International Affective Picture System (IAPS; Lang et al, 2005) and from an additional set of similar images obtained from various sources, primarily internet photography sites. Pictures were equally distributed amongst the three valence categories and positive and negative pictures were matched in terms of arousal level based on normative ratings from a different set of participants. The final data set included; 120 positive (mean valence on a 9 point scale = 7.15, *SEM*=0.01, mean arousal on a 9 point scale = 5.88, *SEM*=0.001), 120 negative (mean valence = 2.80, *SEM*=0.01, mean arousal = 5.89, *SEM*=0.005) and 120 neutral (mean valence = 5.31, *SEM*=0.005, mean arousal = 3.10, *SEM*=0.003). 80 pictures from each valence category (80 positive/80 negative/80 neutral) were shown during the initial study phase and the other 40 (40 positive/40 negative/40 neutral) were distracters during the test phase. In order to avoid order effects, pictures were counterbalanced so that all images were either distracters or studied items.

Verbal paired associates, which were used to test relational memory and cued recall, were compiled using a neutral cue word and affective target word (negative or neutral). Ninety neutral cue words were drawn from the Toronto word pool (Friendly et al, 1982) whereas ninety affective target words (45 negative; mean valence = 2.27, *SEM*=0.01 and mean arousal= 6.24, *SEM*=0.02, and 45 neutral; mean valence = 5.38, *SEM*=0.01 and mean arousal= 4.17, *SEM*=0.02) were drawn from the Affective Norms for English Words (ANEW, Bradley & Lang, 1999). All words were matched in terms of word length (*M* = 5.68, *SEM*=0.02) and word frequency (*M* = 14.30, *SEM*=0.18). Each cue word was randomly paired with one target word, thereby creating a list of ninety pair associates. Word pairs with obvious semantic relationships were re-randomized. The list of paired associates were then randomly divided up into groups of 30, forming three lists: A, B, and C. In order to avoid order effects, the three lists were counterbalanced so that each participant saw the lists in a different order.

A modified version of the original Paced Auditory Serial Addition Task (PASAT; Gronwall, 1977) was used in order to measure vigilance and attention (see Appendix for more detailed description) in all participants. A PASAT-3 (with single digit numbers playing at 3 sec intervals) and PASAT-2 (with single digit numbers playing at 2 sec intervals) were administered and scores from both tests were summed together for a maximum score of 120. 61 single digit numbers were played using PSYSCOPE X (B 53, http://psy.ck.sissa.it/). Two versions of each test were created and counterbalanced across participants.

The North American Adult Reading Test (NAART; Blair & Spreen, 1989) was used to measure general verbal intelligence. The NAART is an oral reading test where individuals are instructed to read a list of 50 words which are irregular in their pronunciation (e.g gaoled). Performance was measured by counting the number of errors in pronunciation (see Appendix for more detailed description).

Three questionnaires were administered to assess subjective alertness (Stanford Sleepness Scale; Hoddes, E. Dement, W. Zarcone, 1972), daytime sleepiness (Epworth Sleepiness Scale; Johns, 1991) and mood at the time of testing (PANAS, Watson et al., 1988) (see Appendix 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.

Procedure

Encoding Tasks

During the encoding period, affective pictures and verbal paired associates were presented sequentially on a Macintosh desktop computer screen using PSYSCOPE X (B

53, http://psy.ck.sissa.it/). To allow for deeper encoding for the picture runs, participants were instructed to indicate whether they would approach or avoid the object or scene depicted in the picture using a Likert-like scale of 1 (move very close) to 5 (move very far away). In order to avoid intentional learning, participants were not informed that the second session would be a memory test.

Each trial began with a white fixation cross in the center of the computer screen for 1000. A picture was then presented in the center of the computer for 1000ms ms with a 1 to 5 number scale presented horizontally underneath the picture and the words "Approach" and "Avoid". The scale remained on the screen for an additional 500 ms after the picture had disappeared. During the 1500 ms interval, participants were asked to indicate whether or not they would approach or avoid whatever was depicted in the picture using the 1-5 number keys on the computer keyboard (Figure 2, for diagram of picture encoding trial).

For verbal paired associates, participants were shown unrelated pairs of words and instructed to visualize a situation in which the two words would go together. In order to allow for deeper encoding, participants would then have to rate how successful they were in forming an association (e.g. visualizing the two words together) using a Likert-like scale of 1 (extremely unsuccessful) to 5 (extremely successful). The entire list of verbal paired associates was presented twice to ensure deeper encoding. In order to avoid intentional learning, participants were not informed that the second session would be a memory test.

Each trial began with a white fixation cross in the center of the computer screen for 1000 ms. A word pair was then presented in the center of the computer for 4000 ms during which the participant would have to try 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”. The scale remained on the screen for 1000 ms 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 (Figure 3, for diagram of Verbal Paired Associates trial).

30-min-delay Tasks

After the encoding tasks all participants underwent various standardized tests to measure vigilance (PASAT), verbal intelligence (NAART) and mood at time of testing (PANAS). After participants completed the questionnaires, they were either excused until the next session (if they were in either 12-hour delay group) or continued on to the memory tests (if they were in either 30 minute delay group). Participants in either 12-hour delay group were asked to keep track of their bedtime and wake time (sleep-delay group) or their activities during the day (wake-delay group). Participants in the wake-delay group were asked not to nap during the delay period.

Memory Tasks

The second session began either immediately after the 30-min delay period or 12 hours after the first session, depending on the condition the participant was assigned to. During this session participants first completed multiple retrieval tasks and then gave subjective ratings of valence and arousal for the materials they have previously viewed. All participants completed all tasks. Cued-recall was administered in order to determine the effect of sleep on emotional associative memory whereas the recognition task was administered in order to determine the effect of sleep on item memory. Additionally, both memory tasks were allowed us to determine the effect of the sleep and emotion interaction on processes of recollection (indexed by both remember responses and cued-recall performance) and familiarity.

Cued Recall Task: Participants were shown the cue word for each verbal paired associate followed by a black space 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.

Recognition Task: Participants were shown the pictures they had seen during the initial study phase along with distracters that were not shown earlier and were asked to judge if the picture was old or new. More specifically, participants were asked to indicate whether they remembered a picture, whether it was familiar to them, or whether the picture was new. For ‘Remember’ responses, participants were instructed to make this judgment if they had previously seen the picture but more importantly, if they could also recollect or remember something specific about the picture’s presentation (e.g. any thoughts, feelings they had) that made them confident that they had been shown the picture in the previous session. In contrast, participants were instructed to make a ‘Familiar’ response if they thought they had seen the picture in the previous session but were unable to recollect any specific information about the picture’s presentation. Finally participants were instructed to respond “New” if they did not think they had seen the picture in the previous session.

Each of the 360 trials began with a white fixation cross (1000 ms) followed by a picture stimulus which remained on the screen until the participant made a Remember/Familiar/New response. Responses were recorded by the experimenter.

Subjective Emotional Ratings

Finally, participants were asked to provide subjective ratings of emotion using both valence and arousal dimensions for all the stimuli they had previously seen. Participants were first instructed to rate whether they found the stimuli negative or positive using a Likert scale of 1 (negative) to 5 (positive). For negative emotions, words like unhappy, angry, sad, disgusted, and scared were used as examples for the negative endpoint whereas happy, pleased and good were used as examples for the positive endpoint. Participants were then instructed to rate how strong they found that emotion 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 rated the pictures they had seen in the original study session and the second, or target, word of each verbal paired associate.

Each picture trial began with a white fixation cross (1000ms) followed by the presentation of the picture (1000ms) in the middle of the computer screen. During this time participants were instructed to just look at the picture. Then the picture would disappear and a 1-5 scale would appear on the bottom of the screen with the words "Negative" and "Positive". Participants had as long as they wanted to respond using the 1-5 keys on the keyboard but were instructed to respond with their initial thought. Once participants made a valence response, another 1-5 scale would appear on the bottom of the screen with the words “Low” and “High”. As with the valence scale, participants had as long as they needed to respond but were instructed to respond with their first thought.

Each verbal paired associate trial began with a white fixation cross (1000ms) followed by the presentation of the second word of each pair (2000ms) in the middle of the computer screen. During this time participants were instructed to just look at the word. Then the word would disappear and a 1-5 scale would appear on the bottom of the screen with the words “Negative” and “Positive”. Participants had as long as they wanted to respond using the 1-5 keys on the keyboard but were instructed to respond with their initial thought. Once participants made a valence response, another 1-5 scale would appear on the bottom of the screen with the words “Low” and “High”. As with the valence scale, participants had as long as they needed to respond but were instructed to respond with their first thought.

Analytic Approach

To study the effects of emotion and sleep on recollection accuracy, as measured with the cued recall task, proportion of correct responses was calculated by dividing the number of correct responses by the number of possible correct responses.

To study the effects of emotion and sleep on the processes underlying the experiences of remembering and knowing, as measured with the picture recognition task, estimates of recollection and familiarity, as derived from the dual-process signal-detection model (Yonelinas & Jacoby, 1994) where computed. Recollection was estimated by subtracting the proportion of remember false alarms (Remember judgments given to new pictures; R_{new}) from the proportion of remember hits (Remember judgments given to old pictures; R_{old}) and then dividing by the proportion of times a participant could have given a Remember judgment correctly. In order to account for the non-independence of remember and familiar responses; familiarity was estimated by subtracting the proportion of times a participant could incorrectly respond “Familiar” to new pictures (F_{new}) if they didn’t respond “Remember” from the proportion of times a participant could respond “Familiar” to an old picture if they didn’t respond “Remember” (F_{old}). F_{new} was calculated by dividing the proportion of familiar false alarms from 1- R_{new} and F_{old} was calculated by dividing the proportion of familiar hits from 1- R_{old}. Finally, general recognition was measure by combining remember and familiar hits and subtracting from false alarms (both remember and familiar false alarms).

Effects of emotion and sleep on the different dependent measure of memory (cued recall, Remember and Familiar judgments) were evaluated with mixed effects analyses of variance (ANOVAs), with group (sleep-delay versus wake-delay) as the between-subject factor and valence (neutral, negative, and positive and neutral and negative for the verbal paired associates) as the within subject factor. Effect size was assessed as general eta squared (η_G^2). Interaction effects were additionally evaluated by applying t-tests. Homogeneity of variance was verified by Levene’s test.

In order verify that any differences in memory performance were not a result of circadian effects, t-tests were performed comparing subjective ratings of alertness (as measured by SSS) and performance on the PASAT. In order to ensure that performance on the cued recall task was not a result of differences in verbal intelligence t-tests were performed comparing performance on the NAART. Scores on the NAART were computed by counting the number of errors of pronunciation, therefore high scores represented poor performance.

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

Circadian Effects on Encoding: Comparison of Morning and Evening Control Groups

In order to determine that there were no time-of-day effects on encoding processes, primarily, we first examined whether circadian effects influenced memory performance on either memory task and found no evidence of such influences. No measure of memory performance differed between the morning and evening 30-min-delay groups (see Tables 1 and 2, for memory performance for the cued-recall task and recognition task). Standard measures of subjective alertness, acquired using the Stanford Sleepiness Scale, also were not significantly different between the morning and evening 30-min-delay groups (*M*= 2.89, *SEM*= 0.31 vs. *M*= 2.22, *SEM*= 0.15, *p*= 0.07). Finally objective measures of vigilance, acquired using the PASAT , were not significantly different between the morning and evening 30-min-delay groups (*M*=114.67, *SEM*= 1.83 vs. *M*=117.11, *SEM*= 0.51, *p*= 0.22). These findings strongly suggest that diurnal differences in cognitive performance, general levels of alertness, or vigilance, do not account for the memory differences we found between the sleep-delay and wake-delay groups.

Effect of Time of Day on Sleep-delay and Wake-delay Conditions

In order to confirm that diurnal differences were not responsible for any observed differences in memory performance between the sleep-delay and wake-delay groups we measured subjective alertness using the Stanford Sleepiness Scale and found no significant differences between groups (*M*=2.50, *SEM*=0.26 vs. *M*= 2.50, *SEM*=0.15, *p*= 1.00). Additionally, objective measures of vigilance, acquired using the PASAT, were not significantly different between the sleep and wake-delay groups (*M*=112.58, *SEM*=3.57 vs. *M*=111.67, *SEM*=2.25, *p*= 0.83).

Some evidence suggests that there diurnal differences in mood (Boivin et al, 1997). 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 significant differences in either affect score for participants in the sleep-delay and wake-delay groups (Table 3, for PANAS scores), suggesting that there were no significant differences in mood between the groups.

Subjective valence and arousal ratings

Subjective valence and arousal ratings were collected from all participants (Tables 4 & 5, for affective ratings). Subjective valence ratings matched normative ratings in that there was little discrepancy between the participants' perception of an item's valence and the experimenter's initial valance classification. Differences in arousal levels for negative (mean on a 5 point scale =3.57, *SEM*=0.11) and neutral (*M*=2.26, *SEM*=0.14) verbal paired associates were significant; *t*(41)= 7.60, *p*<0.0005. Differences in arousal levels for the pictures were also significant. Specifically, negative pictures (*M*=3.31, *SEM*=0.09) differed from both positive (*M*=3.03, *SEM*=0.09); *t*(41)= 3.89, *p*<0.0005 and neutral (*M*=2.32, *SEM*=0.11) pictures; *t*(41)= 7.95, *p*<0.0005, whereas positive pictures also differed from neutral pictures; $t(41) = 7.37$, $p < 0.0005$.

Effect of sleep on memory performance

Associative memory: Cued recall of word pairs

In order to ensure that any enhancement in memory performance for the verbal paired associates was not due to differences in verbal intelligence, an independent means t-test was conducted comparing the sleep-delay and wake-delay groups. There was no significant difference in pronunciation performance (Table 3, for NAART test scores).

A mixed effects ANOVA with emotion (negative vs. neutral) as within-subjects factor and condition (sleep-delay vs. wake-delay) as between-subjects factor was conducted in order to test the effect of sleep on emotional cued recall performance for the verbal paired associates. There was a significant main effect of sleep for proportion correct responses $F(1,22) = 12.25$, $p = 0.002$, $\eta_G^2 = 0.36$ with better cued recall performance observed in participants in the sleep-delay group for both negative ($t(22) = 3.20$ $p < 0.005$) and neutral verbal paired associates $t(22) = 3.61$, $p < 0.005$) (Figure 4, for cued recall performance comparison). There was not a significant main effect emotion for proportion correct responses $F(1,22) = 0.99$, $p = 0.33$, $\eta_G^2 = 0.04$ indicating that there was not a statistically difference in cued-recall performance for negative (*M*=0.34, *SEM*=0.05) and neutral (*M*=0.35, *SEM*=0.05) verbal-paired associates, independent of sleep condition.

The interaction between emotion and condition was not significant $F(1,22) = 0.18$, $p = 0.68$, $\eta_G^2 = 0.01$. Because of the strong *a priori* prediction that sleep would benefit memory preferentially for arousing items relative to neutral items, a median split was performed based on participants' subjective arousal ratings of the negative verbal paired associates. There was no significant difference in arousal ratings between the sleep and wake delay groups and so ratings were combined to create bins. Based on the distribution of the subjective arousal ratings for negative pairs, the top 50% of negatively arousing word pairs (high arousal negative word pairs) where compared to neutral word pairs. A mixed effects ANOVA with emotion (high arousal negative vs. neutral) as within-subjects factor and sleep condition (sleep delay vs. wake delay) as between-subjects factor did not show a significant effect $F(1,22)= 1.58$, $p=0.22$, $\eta_G^2=0.07$ (Figure 5a, for cued recall performance comparison between high negative arousal pairs and neutral pairs). Memory performance was also compared for low arousal negative word pairs and neutral word pairs. A mixed effects ANOVA with emotion (low arousal negative vs. neutral) as within-subjects factor and condition (sleep delay vs. wake delay) as between-subjects factor did not show a significant effect $F(1,22)= 1.15$, $p=0.30$, $\eta_G^2=0.05$ (Figure 5b, for cued recall performance comparison between low negative arousal pairs and neutral pairs).

Item memory: Picture recognition

A mixed effects ANOVA with emotion (negative, positive, and neutral) as within-subjects factor and condition (sleep-delay vs. wake-delay) as between-subjects factor was conducted in order to test the effect of sleep on emotional recognition performance for the pictures. There was no significant main effect of sleep for proportion corrected hits (combining remember and familiar responses) $F(1,22) = 1.00$, $p= 0.33$, $\eta_G^2= 0.04$. There was also no significant main effect of emotion for proportion corrected hits $F(2,44) = 2.80$, $p= 0.07$, $\eta_G^2= 0.11$ (although it approached significance). There was also not a significant interaction between sleep and emotion effect $F(2,44) = 0.95$, $p= 0.40$, $\eta_G^2=$

0.04 (Table 6, for item recognition performance).

In order to further investigate the lack of emotion effect on general recognition performance, a median split was performed based on the subjective arousal ratings for the negative and positive pictures to see if there was an interaction between sleep and emotion. A mixed effects ANOVA with emotion (high arousal negative, high arousal positive, neutral) as within-subjects factor and condition (sleep delay vs. wake delay) as between-subjects factor did not show a significant effect $F(1,22)= 2.26$, $p=0.15$, $\eta_G^2=0.09$ (Figure 6, for overall recognition memory performance). These results suggest that post-learning sleep may not significantly benefit emotional recognition performance. However, recognition performance was at ceiling for both of these conditions (Figure 7a, for uncorrected recognition memory performance) possibly masking any effect of sleep. Any difference between conditions or emotion-type appears to be driven by high false alarm rate (Figure 7b, for false alarm rate for general recognition).

Effect of sleep on remember versus familiar responses

In order to determine if sleep differentially influenced remember and familiar judgments mixed effects ANOVAs were conducted. For corrected remember hits, a mixed effects ANOVA was conducted with emotion (negative, positive, and neutral) as within-subjects factor and condition (sleep-delay vs. wake-delay) as between-subjects factor. There was no significant main effect of sleep for proportion of hits among corrected remember responses $F(1,22) = 0.25$, $p= 0.62$, $\eta_G^2= 0.01$. However there was a significant main effect for emotion (when sleep-delay and wake-delay groups were combined) $F(2,44) = 4.30$, $p= 0.05$, $\eta_G^2= 0.16$ with a larger proportion of corrected remember hits for negative (M=0.63, *SEM*=0.05) than for neutral pictures (*M*=0.60, *SD*=0.22), *t*(23)= 2.32, *p*= 0.03. However, there was not a significant interaction between emotion and sleep condition *F*(2,44) = 4.17, *p*= 0.053, η_G^2= 0.05, although it did approach significance (Figure 8a, for recollection memory performance). Additionally, the resulting independent *t*-test comparing neutral corrected remember hits indicated that the difference in performance between sleep-delay group (*M*= 0.63, *SEM*= 0.07) and wake-delay group (*M*= 0.54, *SEM*= 0.05) was not significant, *t*(22)=1.03, *p*=0.31. Corrected familiar hits responses were compared using mixed effects ANOVA emotion (negative, positive, and neutral) as within-subjects factor and condition (sleep-delay vs. wake-delay) as between-subjects factor. There was no main effect for sleep or emotion and there was no interaction for sleep and emotion (Figure 8b, for familiarity memory performance).

Discussion

The current study investigated differences in memory processing of emotional (negative and positive) arousing stimuli relative to neutral stimuli across a night of sleep and an equivalent period of daytime wakefulness. Contrary to our original hypothesis and previous studies, that have demonstrated that emotional experiences undergo a latent process of amplified consolidation both over time (Sharot & Yonelinas, 2008; McGaugh, 2004), and after a period of sleep (Payne et al, 2008; Hu et al, 2006), we did not observe enhanced memory for emotional items relative to neutral. Rather, memory for neutral items appeared to be enhanced to an equivalent degree relative to emotional items. Consistent with previous literature (Drosopolous et al, 2005; Born & Gais, 2003), we did observe that post-learning sleep enhanced more explicit recollection type memory (as indexed by cued-recall performance) over familiarity-based item memory. Finally, as we were unable to demonstrate an effect of emotion on subsequent memory performance, we were likewise unable to determine if enhancement in subsequent memory differed for negative and positive emotional items. As a whole, these results speak for a greater sensitivity of recollective than familiarity-based memory formation to the enhancing effects of sleep.

The effect of sleep observed in enhanced cued recall cannot be attributed to circadian variations, since there was no difference in memory performance, subjective alertness ratings and vigilance for the morning and evening control groups. Additionally, if enhancement of memory in the sleep-delay group was merely an effect of improved memory performance in the morning, any effect should have been observed for all memory types. However we observed a selective enhancement for only recollective-type memory in the sleep-delay group.

An alternative explanation for the sleep-specific effects is that the lack of interference normally present during waking activities results in a passive rather than proactive state, thus favoring consolidation at night (Wixted, 2004). However this explanation seems unlikely since the benefits of sleep were only observed for recollective-type memory. If the sleep benefit on subsequent memory performance was a result of lack of interference, then sleep should have benefited “remember” and “familiar” responses equally. However, further experimentation is needed in order to determine the influence of sleep on protecting memories from future interference.

Given these considerations, it appears that sleep itself actively influences specific components of memory consolidation, enhancing recollective-type memory. We now consider each of the main experimental findings in more detail.

Benefits of sleep on cued recall performance and recollection

The proportion of correct responses in the sleep-delay group was significantly better for participants in the sleep-delay group compared to the wake-delay group for both negative and neutral word pairs suggesting there might be a more global consolidation of declarative memory during sleep, with respect to emotional versus non-emotional items. Additionally the interaction between sleep and emotion for corrected 'remember' neutral responses approached significance indicating that sleep may enhance recollective-type memory of neutral items and emotional items to an equivalent degree. A lack of power could have prevented us from observing a significant effect for "remember" responses. The overnight preferential enhancement of recall and, to a lesser degree, recollection performance in somewhat in line with our original hypothesis; that sleep would preferentially enhance recollection over familiarity, and consistent with the view that consolidation of the different types of the different memory representations (recollection vs. familiarity) are differentially influenced by sleep (Rauchs et al, 2004; Born & Gais, 2003; Drosopolous et al, 2005).

Drosopoulos et al (2005) demonstrated that sleep preferentially enhanced recollection of neutral material, where the original episode and specific details associated with the original episode are remembered, over familiarity, which emerges in the absence of any conscious information about the context in which the event occurred. Gais et al (2006) showed a similar sleep benefit for vocabulary free recall performance. Recall, like recollection processes in recognition memory, is a stronger memory trace that involves memory of the original episode along with information about the context in which the event occurred. Finally, Ellenbogen et al (2006b) showed a sleep benefit for cued recall performance of neutral verbal paired associates. Together these findings tentatively suggest that sleep preferentially enhances recollective-type memory over familiarity.

Effect of sleep on emotional declarative memory consolidation

Intriguingly, sleep did not preferentially benefit emotional memory in any of the memory tasks, which is curious given that established literature demonstrates that emotional experiences are undergo amplified consolidation over time (Sharot & Yonelinas, 2008; McGaugh, 2004), and over sleep (Payne et al, 2008; Hu et al, 2006). For the cued recall task, memory accuracy in the sleep delay group was equivalent for the negative and neutral verbal paired associates. The same pattern was observed in recollection performance (as measured by corrected 'remember' hits in the recognition task), where emotional and neutral pictures where recollected to an equivalent degree in the sleep-delay group, relative to the wake-group that saw a decrease in recollection for neutral items. These results indicate that sleep may not preferentially enhance memory for emotional information, possibly calling previous results into question.

There are various explanations for the current results. Firstly, it is possible that sleep and emotion modulate memory consolidation through different pathways. We observed a significant main effect of emotion for corrected remember hits, independent of sleep that is consistent with previous evidence that emotional items will be better remembered relative to neutral. It has been found that this selective enhancement of emotional information relative to neutral is likely due to increased interaction between the hippocampus and amygdala at encoding (LaBar & Cabeza, 2006, Dolcos et al, 2004). Whether the same areas reactivated during subsequent sleep to consolidate emotional memories remains unknown (reviewed in Atienza & Cantero, 2008). Previous studies have found that hippocampal reactivation during sleep could be a key mechanism for memory consolidation of material that is later recollected (Peigneux et al, 2004). Converging evidence also suggests that hippocampal activation selectively increased recollection of emotional items at retrieval (Dolcos et al, 2005).

Therefore, is possible that enhancement in memory for emotional arousing stimuli could depend on interactions between the amygdala and hippocampus during encoding and reactivation of some of these networks during sleep. (reviewed in Atienza & Cantero, 2008) Two recent sleep deprivation studies showed that sleep deprivation only impaired memory performance for positive items and, to a greater degree, neutral items suggesting that a different pathway is at work (Atienza & Cantero, 2008; Sterpenich et al, 2007). Using fMRI, Sterpenich et al (2007) scanned participants during the study phase and during the testing phase, which occurred after 72 hours after study during which participants were sleep deprived, and concluded that increased activation in the hippocampus and cortex during sleep led to increased recollection whereas interactions between the amygdala and cortex could modulate consolidation of emotional information. This suggests that sleep and emotion could modulate memory consolidation through different mechanisms and account for the selective enhancement of neutral recollection (measured by remember hits) after post-learning sleep.

However, it is possible that this alternate pathway for processing emotional information could reflect compensatory mechanisms as a result of sleep-depriving participants. Sleep deprivation experiments could introduce various confounding factors, such as memory impairment due to increased stress from to prolonged wakefulness. Our current results are unable to determine whether there is an interaction or additive effect of sleep and emotion on memory consolidation, or whether sleep and emotion modulate consolidation through different processes.

Alternative explanations for the observed results exist when the two memory tasks are examined separately. One explanation for absent enhancement in emotional memory for the cued recall task could be that participants did not find the negative verbal-paired associates emotionally arousing; despite having selected negative normed words within each word pair to make an emotionally arousing word pair. However, subjective ratings indicate that this is not the case as there was a significant difference in arousal rating responses between negative pairs and neutral pairs, with perceived arousal in negative pair being much higher.

Alternatively, it is possible that some other attribute of the verbal paired associates, lead to selectively enhanced subsequent recall. Theories regarding emotion and memory suggest that emotion leads to a narrowing of attention for the most salient items in a complex scene (reviewed in Oschner, 2000; Waring & Kensinger, 2009; McGaugh, 2000). Specifically, that emotion will increase the distinctiveness of a scene, increasing attention at learning and enhanced subsequent memory performance for those distinctive emotional items. However, it could be argued that it is not the affective value of emotionally arousing stimuli that make them more distinctive, but rather some other property that they may share non-arousing stimuli (discussed in Ochsner, 2000). Affective stimuli are 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.

The verbal paired associates in the current study were created to contain two unrelated words (e.g. CAMEL-MURDERER versus HIGHWAY-DICE) in order to ensure that there were no preexisting associations between words in a pair prior to the study period. Therefore, it is possible that perceived incongruence between words in a pair, or the novelty in the association created lead to improved subsequent cued-recall performance after sleep. Pickel (1998) found that the unusualness of a scene, independent of emotion, could lead to improved subsequent memory performance. However, in the current experiment no ratings for unusualness were collected preventing us from testing this alternate hypothesis. Therefore, in addition to replicating the current study with additional stimuli that may better elicit emotional arousal, future studies could investigate whether emotion is the most salient information that is consolidated during sleep or whether some other attribute, like unusualness may account for effects observed in the current study and in previous studies that demonstrated amplified sleep-dependent consolidation for emotional items.

One explanation for the lack of a significant emotion effect after sleep for the recognition task could be that the recognition task was too easy for participants, leading to ceiling effects that might mask any significant difference in recognition performance between emotional items and neutral items, and between negative items and positive items. In fact, overall hits (where remember and familiar responses were combined) performance was at ceiling for all three valence categories (Figure 7a) despite pilot testing modifying picture presentation time at study to prevent ceiling effects. Additionally, false alarm rate (number of times participants responded “old” to a picture they had not seen before) was relatively high for all valence categories further masking any significant differences in emotional memory performance between the two groups (Figure 7b). Remember responses showed a similar pattern for uncorrected hits (Figure 9a, for remember hits performance) though false alarm rates were low (Figure 9b). Further testing, with a more difficult recognition task is needed to ensure that the lack of influence of emotion on sleep-dependent memory consolidation is not due to task difficulty.

Effect of sleep on associative declarative memory

The primary aim of the study was not to compare associative and item memory and the current design did not allow for a quantitative comparison between the two memory processes. However, by measuring associative memory with the cued recall task, we are able to verify previous claims (Ellenbogen et al, 2006a, 2007) regarding the effect of sleep on associative declarative memory. Relational memory, which is the flexible ability to generalize across existing stores of information, is a fundamental property of human cognition and yet little is known about how and when this inferential knowledge emerges. Recent evidence concerning the consolidation of verbal paired-associates suggests that the development of relational memory evolves "offline" (over time and without further training) and during sleep (Ellenbogen et al, 2006a, 2007). Recent research also demonstrates that sleep enhances memory associations (Stickgold et al, 1999) and the relational building of component motor-sequence memories (Cohen et al, 2005) suggesting that sleep facilitates associative integration of information.

Furthermore, numerous studies emphasize the dependence of association on the hippocampus (Eichenbaum, 2004), which is also consistently implicated in offline memory processing after learning (for review, see Ellenbogen et al, 2006b). Therefore, in addition to strengthening individual item memory, the hippocampus may increase binding and subsequent flexible use of acquired declarative memories, possibly during sleep.

The results of the current study confirm the idea that sleep may strengthen associations between previously unrelated material (e.g. two unrelated words). Performance in the sleep-delay group was significantly higher relative to the wake-delay group, suggesting that sleep may strengthen previously formed associations. Ellenbogen et al, (2006a) tested neutral associative memory and found that sleep enhanced memory for previously formed associations, confirming our findings. Ellenbogen et al, also found that sleep protected these associations from new information that might interference with the association, something that we were unable to test in our current design.

Conclusions

The current study confirmed previous findings that post-learning sleep selectively enhances recall and possibly recollection-based recognition memory over familiarity-based memory. However, contrary to previous literature, this enhancement was not magnified for emotional information, but rather enhanced to an equivalent degree for emotional and neutral items for cued recall and possibly, to a lesser extent, recollection processes of emotion. Our results confirm previous findings that sleep enhances overall memory performance. However, previous work has also demonstrated a preferential enhancement of emotional memory relative to neutral, which we did not observe for cued recall performance and were unable to fully determine in recognition memory performance. Finally our results confirmed established literature that sleep enhances associative memory. Therefore, although the results of the current study were unable to determine whether sleep preferentially consolidates emotional information, findings that sleep enhanced more vivid traces of memory (indexed by recall performance) and associative memory begin to shed light on what type of information is consolidated during sleep.

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Table 1

Associative Memory Performance for Verbal Paired Associates

	Group					
	Morning		Evening		Difference	
Memory Type	*M*	*SEM*	*M*	*SEM*	*t(16)*	*p*
Overall	0.63	0.06	0.54	0.06	1.20	0.25
Negative Pairs	0.64	0.06	0.54	0.07	1.08	0.30
Neutral Pairs	0.62	0.06	0.53	0.05	1.14	0.27

Note. Mean proportion of correctly recalled verbal paired associates in the morning and evening 30-min control conditions. Overall performance (for both negative and neutral pairs), negative pair performance, and neutral pair performance are all reported.

Table 2

Item Memory Performance for Pictures for Morning and Evening 30-Min Conditions

	Group					
	Morning		Evening		Difference	
Memory Type	*M*	*SEM*	*M*	*SEM*	*t(16)*	*p*
Corrected Combined Hits						
Overall	0.75	0.05	0.77	0.04	-0.44	0.67
Negative	0.74	0.07	0.74	0.08	0.01	0.99
Positive	0.77	0.05	0.80	0.07	-0.34	0.47
Neutral	0.67	0.07	0.74	0.07	-0.72	0.48
Corrected “Remember” Hits						
Overall	0.70	0.07	0.71	0.06	-0.14	0.89
Negative	0.69	0.07	0.70	0.07	-0.05	0.96
Positive	0.75	0.06	0.75	0.06	-0.09	0.93
Neutral	0.67	0.09	0.69	0.06	-0.20	0.85
Corrected “Familiar” Hits						
Overall	0.54	0.05	0.53	0.07	0.19	0.85
Negative	0.54	0.06	0.49	0.07	0.52	0.61
Positive	0.56	0.06	0.59	0.11	-0.20	0.85
Neutral	0.52	0.06	0.54	0.06	-0.19	0.85

Note. Mean proportion of correctly recognized pictures in the morning and evening 30-min control conditions. Corrected scores were calculated by subtracting false alarms from hits. Overall recognition performance (remember and familiar corrected hits) is reported first. Then recognition memory is broken down into recollection (indexed by corrected remember hits) and familiarity (indexed by corrected familiar hits).

Table 3

Test scores for PANAS and NAART for Sleep-Delay and Wake-delay Conditions

	Group					
	Sleep		Wake		Difference	
Test	*M*	*SEM*	*M*	*SEM*	*t(22)*	*p*
NAART	11.42	1.23	14.25	1.76	-1.32	0.20
PANAS						
Positive Affect	26.75	2.44	28.00	2.32	-0.37	0.71
Negative Affect	11.50	0.67	11.75	0.66	-0.27	0.79

Note. NAART test score reflects number of pronunciation errors, of 50 words. PANAS test score is divided into Positive Affect (measured by adding Likert-responses to 10 words representing positive affect) and Negative Affect (measured by adding Likert-responses to 10 words representing negative affect).

Table 4

Mean Subjective Valence for Verbal Paired Associates and Pictures

	Emotion					
	Negative		Positive		Neutral	
Group	*M*	*SEM*	*M*	*SEM*	*M*	*SEM*
Verbal Paired Associates						
Sleep-delay	1.73	0.11			3.20	0.08
Wake-delay	1.46	0.07			3.21	0.07
Morning Control	1.42	0.12			3.38	0.13
Evening Control	1.60	0.08			3.16	0.05
Pictures						
Sleep-delay	2.27	0.15	3.52	0.12	3.04	0.05
Wake-delay	2.10	0.23	3.70	0.19	3.18	0.07
Morning Control	1.70	0.13	4.06	0.10	3.18	0.11
Evening Control	1.80	0.11	3.94	0.14	3.12	0.05

Note: Valence ratings were calculated on a 5 point Likert-scale. Ratings are separated by condition.

Table 5

Mean Subjective Arousal Ratings for Verbal Paired Associates and Pictures

	Emotion					
	Negative		Positive		Neutral	
Group	*M*	*SEM*	*M*	*SEM*	*M*	*SEM*
Verbal Paired Associates						
Sleep-delay	3.37	0.18			2.21	0.20
Wake-delay	3.69	0.27			2.17	0.29
Morning Control	3.69	0.18			2.17	0.27
Evening Control	3.55	0.22			2.53	0.41
Pictures						
Sleep-delay	3.02*	0.15	2.92	0.15	2.27	0.20
Wake-delay	3.49*	0.15	3.17	0.18	2.36	0.22
Morning Control	3.50	0.16	3.09	0.17	2.22	0.14
Evening Control	3.29	0.21	2.95	0.27	2.42	0.31

Note: Arousal ratings were calculated on a 5 point Likert-scale. Ratings are separated by condition.. *indicates that scores are significant from each other at $p<0.05$

Table 6

Item Recognition Performance for Sleep-delay and Wake-delay Conditions

	Group					
	Sleep-delay		Wake-delay		Difference	
Memory Type	*M*	*SEM*	*M*	*SEM*	*t(22)*	*p*
Corrected Overall Hits						
Overall	0.67	0.06	0.66	0.06	0.08	0.94
Negative	0.69	0.03	0.68	0.04	0.32	0.75
Positive	0.71	0.05	0.67	0.02	0.67	0.51
Neutral	0.68	0.04	0.58	0.05	1.40	0.17
Corrected Remember Hits						
Overall	0.64	0.06	0.60	0.05	0.53	0.60
Negative	0.63	0.05	0.65	0.04	-0.34	0.74
Positive	0.65	0.06	0.61	0.05	0.51	0.62
Neutral	0.63	0.07	0.54	0.05	1.03	0.31
Corrected Familiar Hits						
Overall	0.48	0.05	0.43	0.05	0.66	0.52
Negative	0.50	0.05	0.44	0.06	0.73	0.48
Positive	0.46	0.07	0.45	0.05	0.19	0.85
Neutral	0.50	0.06	0.41	0.06	1.09	0.29

Note. Overall hit performance is reflected in the corrected number of old hits (combining remember and familiar corrected hits). Recognition performance was then further broken down into recollection (indexed by corrected remember hits) and familiarity (indexed by corrected familiar hits). No differences between groups were significant

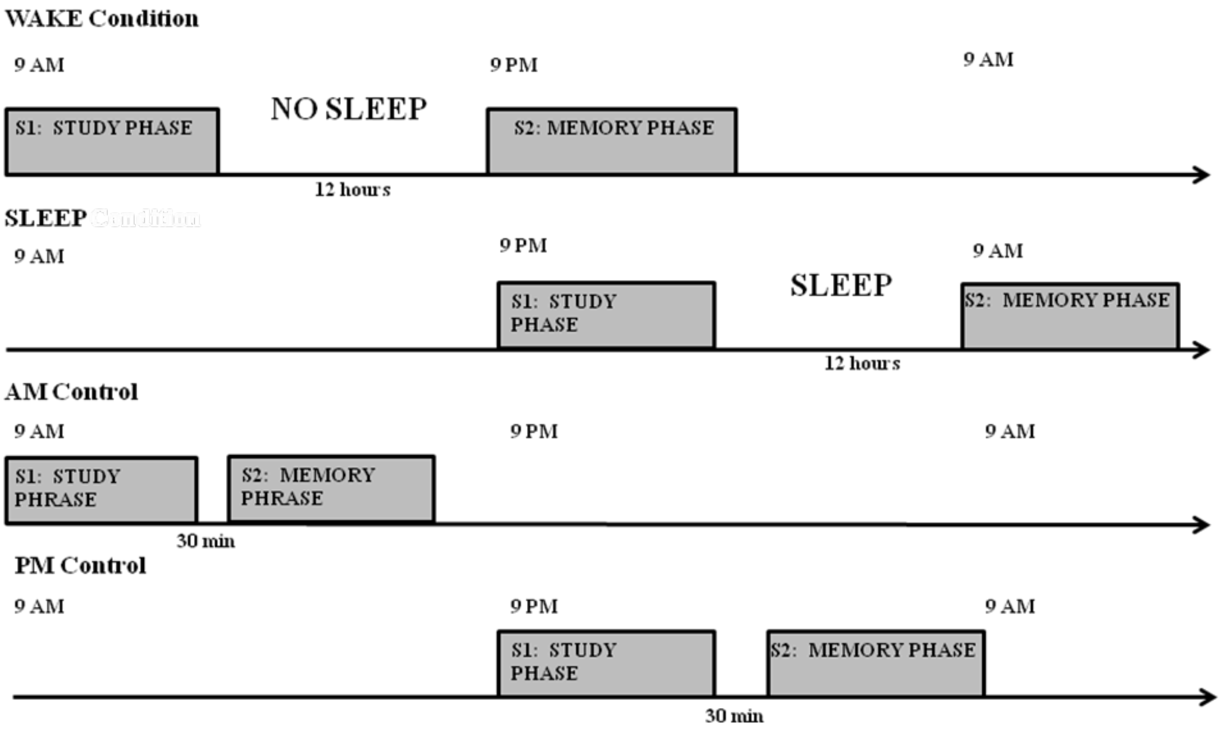

Figure 1. Diagram of Experimental Conditions

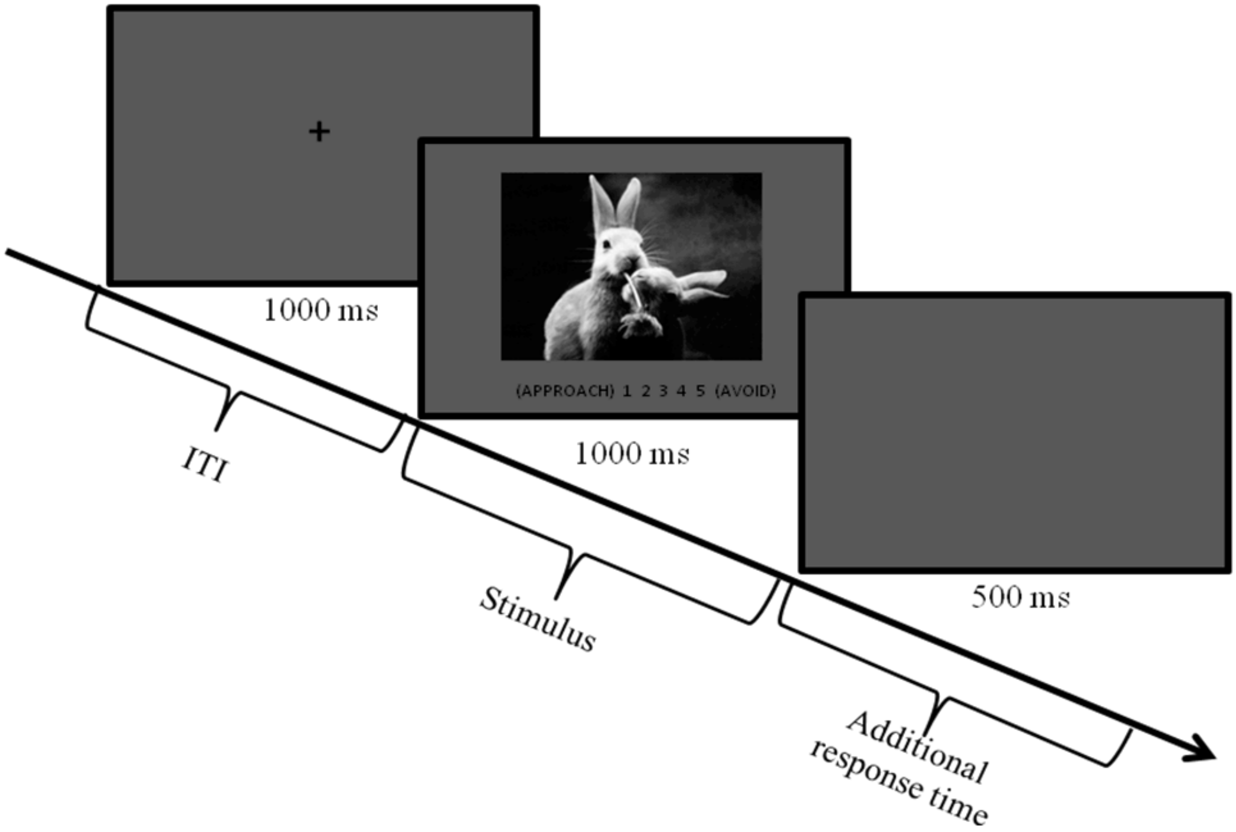

Figure 2. Diagram of Picture Encoding Trial.

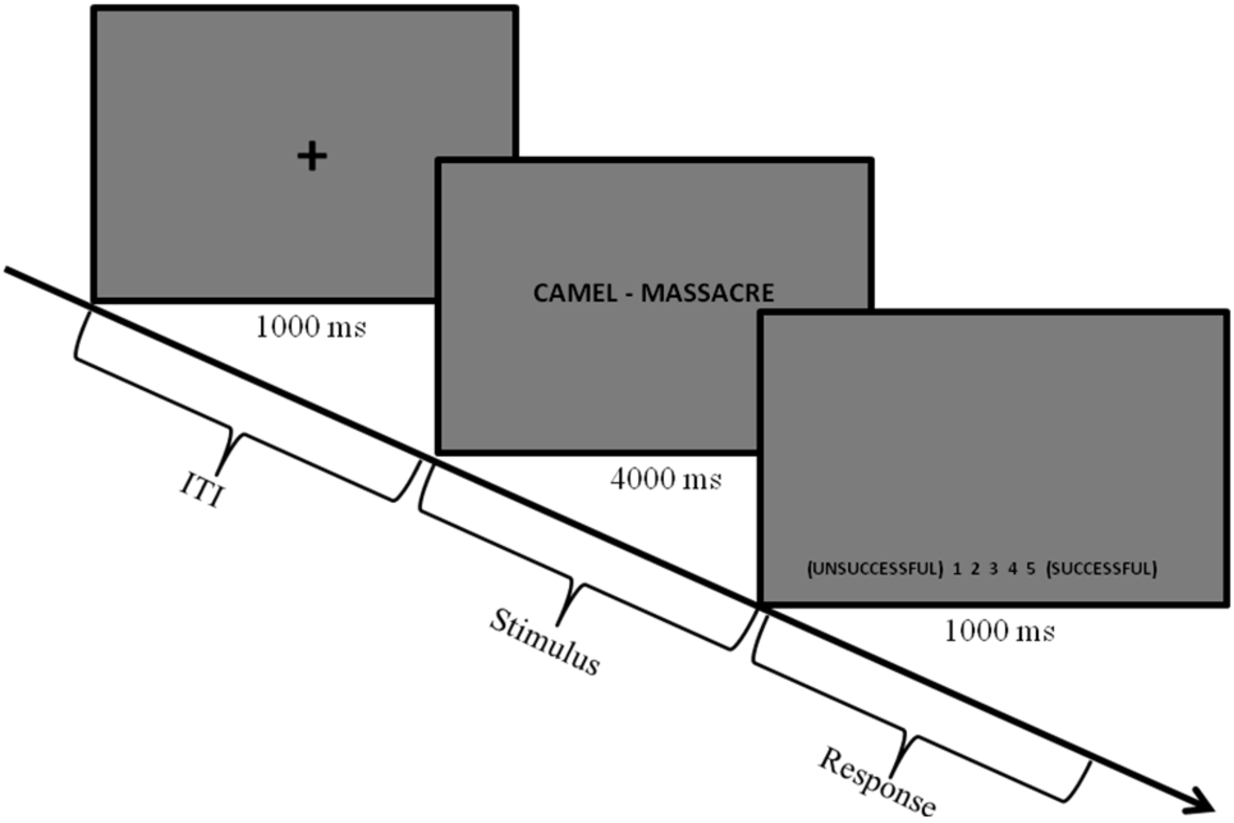

Figure 3. Diagram of Verbal Paired Associates Trial

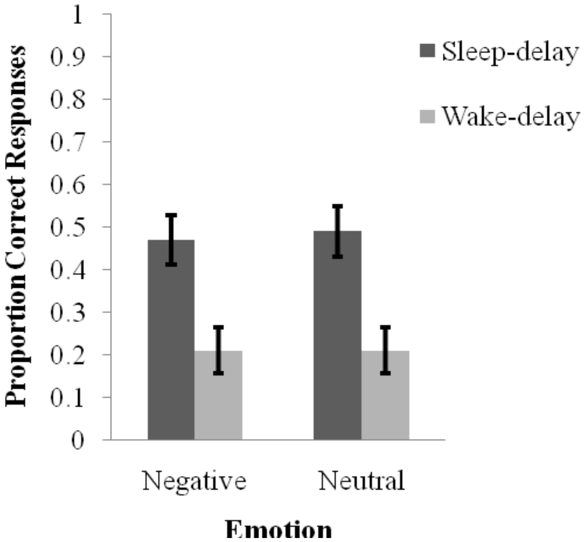

Figure 4. Verbal paired associates cued recall performance for sleep-delay and wake-delay conditions. Proportion correct responses organized by emotion (negative vs. neutral) for sleep-delay and wake-delay groups. No significant differences within conditions (for emotion). All differences between sleep-delay and wake-delay were significant at p< 0.005

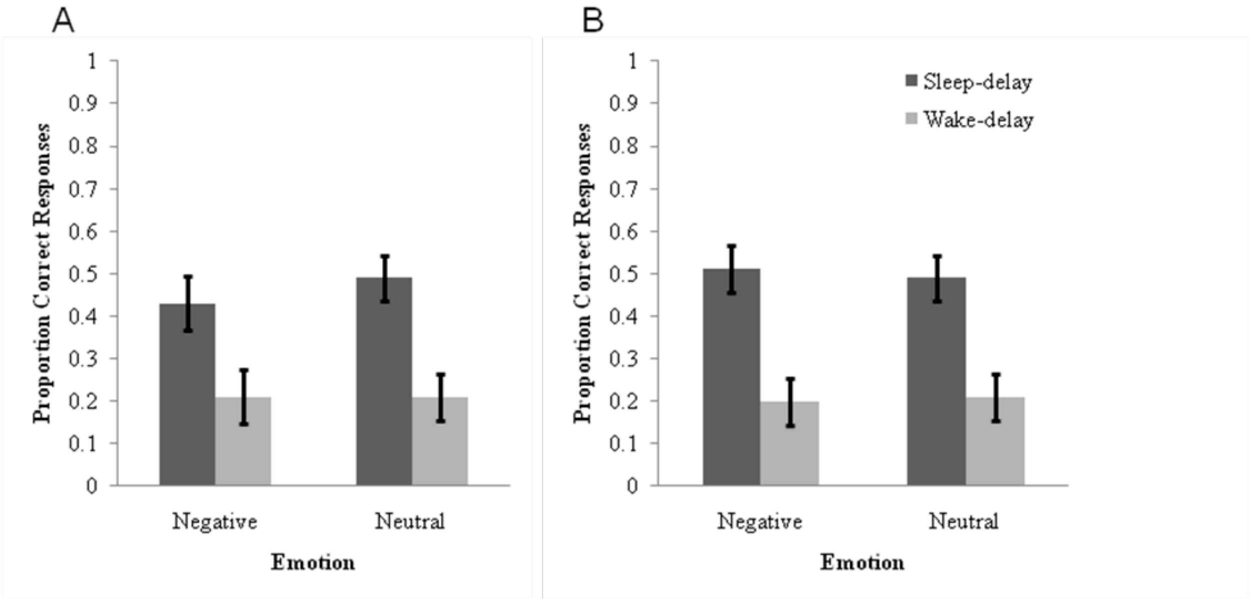

Figure 5. Verbal paired associates cued recall performance for sleep-delay and wake-delay conditions. A) Comparison between high arousal negative pairs vs. neutral pairs. B) Comparison between low arousal negative pairs vs. neutral pairs. No significant differences within groups (for emotion). Differences between sleep-delay and wake-delay groups were significant at $p< 0.00.5$

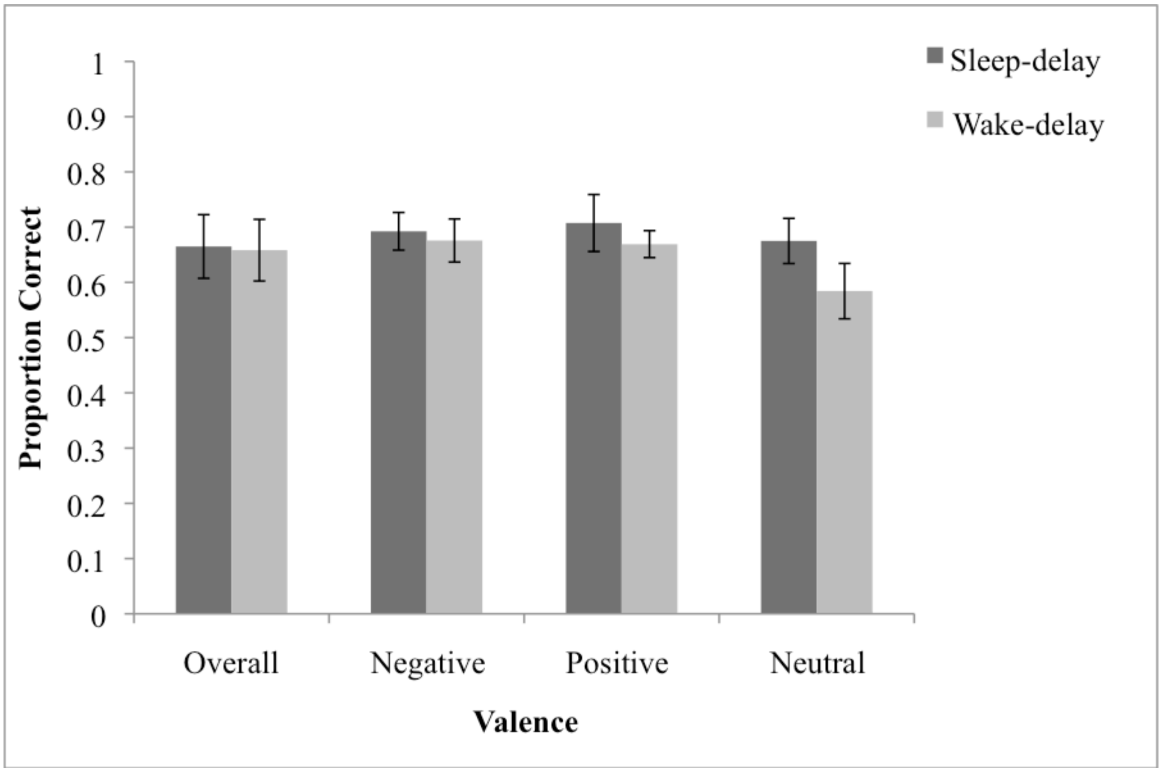

Figure 6. General corrected item recognition performance (combining remember and familiar responses) for sleep and wake-delay groups. All differences between sleep-delay and wake-delay group were not significant. All differences with groups were also not significant.

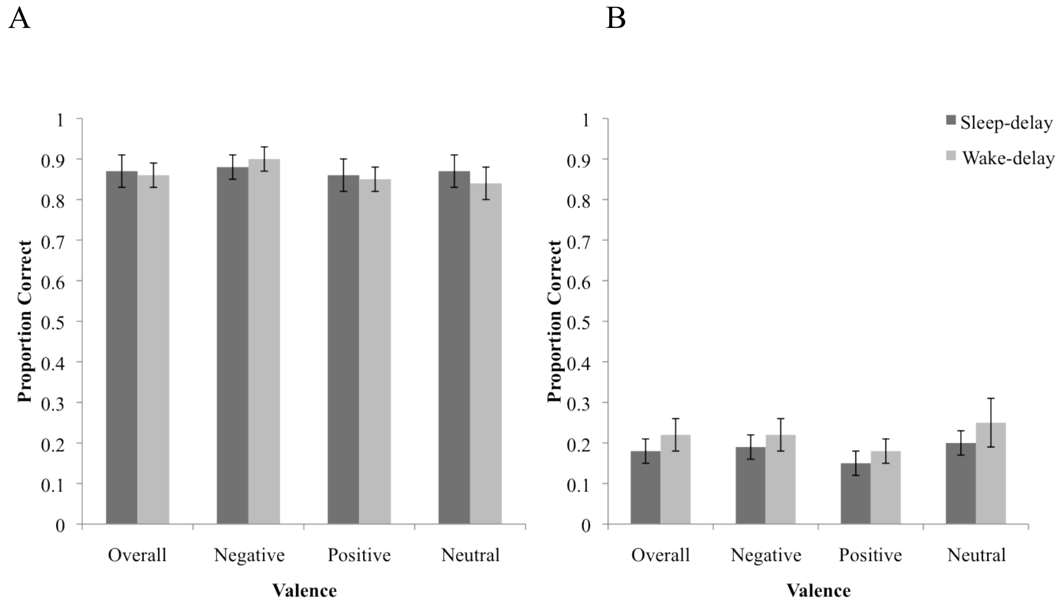

Figure 7. General recognition performance broken down by uncorrected hits and false alarms for sleep-delay and wake-delay conditions. A) Proportion uncorrected hit responses (combined remember and familiar responses) organized by emotion (negative vs. positive vs. neutral). Performance was at ceiling. B) Proportion false alarms (combined remember and familiar responses) organized by emotion (negative vs. positive vs. neutral). Because false alarm rate was relatively high, corrected hit performance were used for final analyses. All differences between conditions were not significant. All differences within conditions were also not significant.

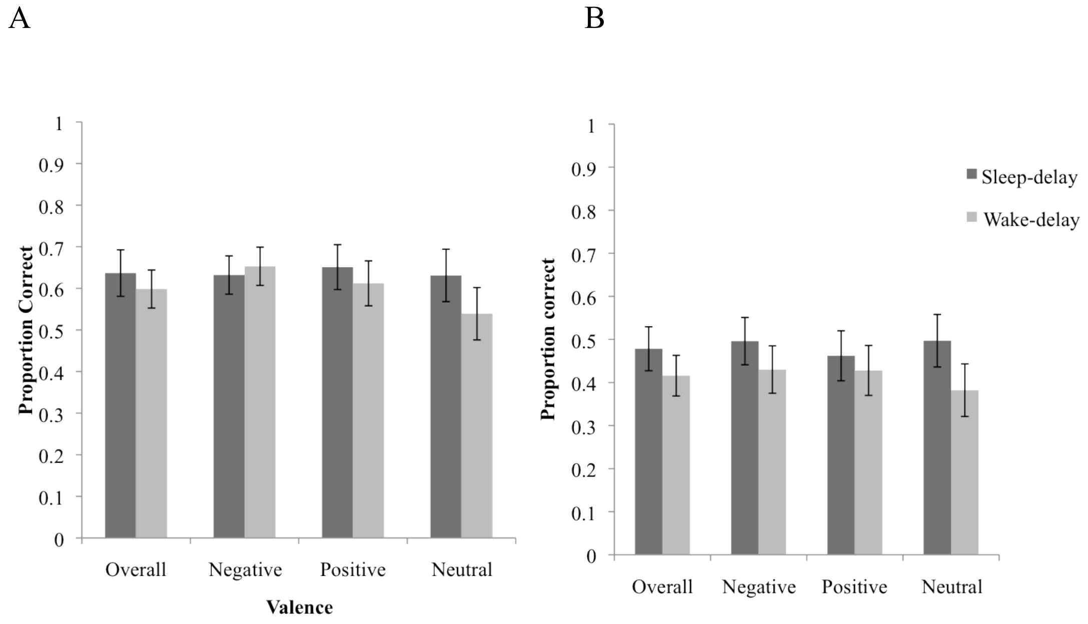

Figure 8. Corrected item recognition performance for sleep-delay and wake-delay conditions, broken down by recollection (indexed by corrected remember responses) and familiarity (indexed by corrected familiar responses). A) Corrected remember hit responses, B) Corrected familiar hit responses.

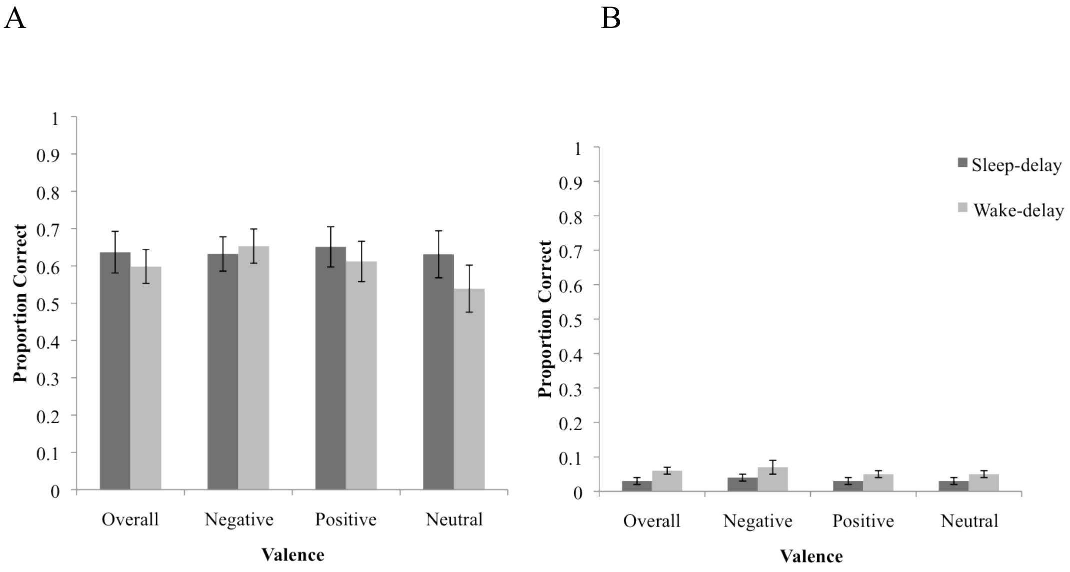

Figure 9. Recollection performance broken down by uncorrected remember hits and false alarms for sleep-delay and wake-delay conditions. A) Proportion uncorrected remember hit responses organized by emotion (negative vs. positive vs. neutral). Performance was close to ceiling. B) Proportion false alarms.

Appendix

PANAS: Positive and Negative Affect Schedule (Watson et al., 1988)

The PANAS measures positive and negative mood. It consists of 20 items, with 10 items addressing positive mood and 10 items addressing negative mood. These scales, which index positive and negative mood, were selected as equivalent 'state' scales of the personality factors extraversion and neuroticism, respectively.

PANAS items are rated on a five-point Likert-type scale (ranging from 'very slightly' to 'extremely') and some example items are as follows: interested (positive), excited (positive), irritable (negative), and ashamed (negative). Depending on the instruction, the scales can be used to assess general mood (e.g., I generally feel this way), or mood at certain times (e.g., I felt this way during the past week, I feel this way now). Empirical evidence indicates that the scales are internally consistent (.84 and .90, alpha coefficients), they are shown to exhibit good test retest reliability (.39 and .71), and they are largely uncorrelated (-.12 and -.23).

PASAT: Paced Auditory Serial Addition Task, (Gronwall, 1977)

The PASAT is … used to measure attention or vigilance. 61 single digit numbers are presented every 3 second followed by a second test where numbers are presented every 2 seconds.

Vigilance was tested using a modified version of the Paced Auditory Serial Addition Task (PASAT; Gronwall, 1977). Participants heard 61 single digit numbers presented every 3 seconds followed by a second test where numbers were presented every 2 seconds. Participants were instructed to add the first two numbers together and then continue adding the number they just heard to the number that directed preceded it. For example, if the first two numbers were '5' and '7', the correct response was '12'. If the next number was then '3', the correct response would be '10'. Correct responses from both tests were then summed together for a maximum score of 120. The PASAT has demonstrated high split-half reliability (r = 0.96). PASAT has relatively strong correlations with other tests of attention, such as Visual Search and Attention Task (r=0.55) and TrailMaking Test B (r=0.58). Test-retest reliability is .93-.97

NAART: North American Adult Reading Test, (Blair & Spreen, 1989)

The NAART is an oral reading test used to measure verbal intelligence. Performance on the NAART is comparable to performance on the Wechsler Adult Intelligence Scale revised (WAIS-R; Wechsler, 1981) Vocabulary test. It consists of a list of 50 words which are irregular in their pronunciation (e.g. gaoled). Performance is measured by counting the number of errors in pronunciation. Empirical evidence indicates that that NAART scores are internally consistent (.93, alpha coefficients), they are shown to exhibit good test retest reliability (.89, 93 and .98), and is moderately to highly corrected (0.4-0.8) with other measures of general intellectual status.