May 2023

The Effect of Sleep and Emotion on Pattern Separation

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THE EFFECT OF SLEEP AND EMOTION ON PATTERN SEPARATION

By

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Bachelor of Science – Psychological Science
Montana State University
2020

A thesis submitted in partial fulfillment
of the requirements for the

Master of Arts – Psychological and Brain Sciences

Department of Psychology
College of Liberal Arts
The Graduate College

University of Nevada, Las Vegas
May 2023

Thesis Approval

The Graduate College
The University of Nevada, Las Vegas

April 4, 2023

This thesis prepared by

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entitled

The Effect of Sleep and Emotion on Pattern Separation

is approved in partial fulfillment of the requirements for the degree of

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Abstract

Prior work on the relationship between sleep and memory suggests that the sleep state is an optimal time for memory consolidation to occur. During slow wave sleep, newly encoded information in the hippocampus is repeatedly activated, driven by slow oscillations that originate in the neocortex. This process that occurs during slow wave sleep facilitates the long-term storage of memories. A widely accepted view of emotion and sleep is that emotional memories are preferentially consolidated during sleep so that they are easily accessible for retrieval, whereas neutral memories tend to be less accessible. However, recent meta-analyses of sleep, emotion, and memory have suggested that this effect may not be as robust as we once thought. To address this issue, the current study investigated the influence of sleep on the consolidation of emotional and neutral memories in a pattern separation task. The results showed no difference between the sleep and wake group on measures of pattern separation or item recognition and no preferential consolidation of emotional images over neutral images. These findings contradict prior literature, but raise questions about the role of sleep in memory consolidation, and more specifically, emotional memory consolidation.

Acknowledgements

I would like to acknowledge my advisor, Dr. Colleen Parks. Her support and guidance knows no bounds. I would also like to acknowledge my research assistants in the Human Memory Lab for all their hard work assisting me with data collection.

Dedication

This thesis is sincerely dedicated to the people who have supported me throughout my education experience. I cannot thank my parents, loving partner, and amazing peers in the Human Memory Lab enough.

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Chapter 1: Introduction

"Encoding and retrieval occur in the awake state, but adequate sleep improves all stages of memory formation, particularly consolidation and reconsolidation," (Miglis, 2017). For many years, this view of sleep and memory has remained prevalent among researchers in the field. In the early 1900's, Rose Heine showed that subjects who learned stimuli in the evening before sleep had less forgetting than learning before an interval of wakefulness (Rasch & Born, 2013). This observation was the first indication of the importance of sleep for memory. After many decades of developing and testing theories, it is widely believed that sleep plays a crucial role in memory consolidation, but the underlying mechanisms are not well understood.

Sleep is defined as a natural and reversible state of reduced responsiveness to external stimuli and relative inactivity accompanied by a loss of consciousness (Rasch & Born, 2013). There are two main stages of sleep: sleep without rapid eye movements (NREM) and sleep with rapid eye movements (REM). Within NREM sleep, there are three stages of sleep: N1, N2, and N3 sleep. N1 is experienced when wakefulness transitions to sleep, N2 is a period of light sleep before you enter deeper sleep, and N3, often referred to as slow wave sleep (SWS) is the deepest stage of sleep within NREM.

When a memory is first encoded it is in a labile state. Under the right conditions, it undergoes consolidation, which is the process of memory stabilization over time, making it more resistant to interference or disruption (Walker, 2009). Alvarez and Squire (1994) argue that the medial temporal lobe (MTL) plays an important role in memory consolidation. For example, they postulated that the hippocampus acts as a temporary memory store for new memories, while the neocortex serves as a permanent memory store. They also argue that the hippocampus does not store information, but rather acts as an orienting system that signals to the neocortex the need to form a new representation.

Sleep and Memory

The examination of the relationship between sleep and memory consolidation suggests that the sleep state is an optimal time for memory consolidation to occur. Slow wave sleep has been considered important for memory consolidation, most commonly through a model known as active systems consolidation. Active systems consolidation refers to the process by which newly encoded memory representations are redistributed to other neuron networks, which is a common term used to describe how memories are consolidated when the brain is in a wake state, but has different implications for the brain in a sleep state (Born & Wilhelm, 2012). The active system consolidation during sleep theory posits that memories are reactivated during sleep to be consolidated, that the consolidation process during sleep is selective, and memories undergo qualitative changes when transferred to long-term store. During slow wave sleep, newly encoded information in the hippocampus is repeatedly activated, driven by slow oscillations that originate in the neocortex (Walker, 2009; see also Carr et al., 2011 for evidence of replay in a wake state). This process that occurs during slow wave sleep facilitates the long-term storage of memories.

There are several studies that demonstrate that sleep is critical to consolidation. In 2006, Ellenbogen et al. performed the first study that demonstrated that sleep-facilitated consolidation protects declarative memories from subsequent associative interference. Participants learned a list of word pairs (A-B) followed by a 12-hour retention period consisting of sleep or wakefulness. Prior to the cued recall, participants in the interference condition learned a new list of word pairs (A-C), whereas participants in the no-interference condition went directly to testing. In the no-interference condition, the mean recall of word-pairs was marginally higher in the sleep group than the wake group, and in the interference condition, there was a significant difference between mean recall of word pairs in the sleep group than the wake group. The authors proposed that sleep plays an active role in consolidating declarative memories, which makes them resistant to interference.

Since this experiment, several other studies have been published examining sleep and declarative memories (e.g., Backhaus et al., 2008, Feld et al., 2016, Sonni & Spencer, 2015, Schönauer et al. 2014). However, sleep and memory research is not without challenges. A recent attempt to replicate the results found by Ellenbogen et al. in 2006 did not show an effect of sleep protecting memories against retroactive interference. Bailes et al. (2020) set out to clarify whether sleep merely slows the forgetting that would otherwise occur as a result of information processing during wakefulness, or whether sleep actually facilitates the consolidation of memories, protecting them from subsequent retroactive interference. By using the same paired-associates task as Ellenbogen et al. (2006), memory for word pairs was tested after a 12-hour interval. The results indicated that those who slept during the interval had better memory for the word-pairs than those who were awake, but they did not replicate the observation of a large effect of sleep in protecting memories against interference learning.

Pöhlchen et al. (2020) also aimed to replicate the finding that sleep protects memories from retroactive interference. They performed two experiments; one used an afternoon nap design and the other used a period of nighttime sleep or daytime wake. Following the protocol used by Ellenbogen et al. (2009), subjects learned a list of 60 word pairs (A-B) followed by the designated retention interval. They then learned an interfering list of word pairs (A-C) and were tested on the original list. The results from both experiments indicated that there was no protective effect of sleep on memory as had been reported by Ellenbogen et al. (2009). The findings from these studies suggest that future research is needed before drawing strong conclusions about the role of sleep in stabilizing memories against interference.

These replication failures have raised further questions about the relationship between sleep and memory. Cordi and Rasch (2020) reviewed and summarized evidence by highlighting recently published replication failures for the beneficial effect of sleep on memory. The authors claim that we cannot conclude based on the reported null-findings that the beneficial effect of sleep on memory does not exist, but rather that these findings demonstrate that this effect is smaller, more task-specific, less robust, and less long-lasting than previously assumed.

A similar paper was published by Dastgheib et al. (2022), suggesting that sleep does not play a "critical" role in consolidation, but rather, sleep falls along a continuum of behavioral states that vary in their effectiveness to support memory consolidation at the neural and behavioral level. This article highlights a prevalent controversy in the sleep and memory field: is memory consolidation similar in waking and sleep? Many articles have investigated this claim, and present similar conclusions.

Siegel (2021) argued that memory consolidation clearly occurs in both sleep and waking, and whether consolidation might differ in these two states has not been conclusively determined. He challenges the interference paradigm, specifically sleep deprivation paradigms, stating that individuals in wake groups will forget more simply due to the fact that they are exposed to more information. This comes about by inevitably interacting with the laboratory environment. As a result, participants may be less able to recall the particular items the experimenter is measuring which can then mistakenly lead to the conclusion that sleep is required for memory consolidation. He further states that individuals that are in a quiet waking period where the environment is being ignored typically produce a gain in recall that is similar to sleep.

Similarly, Dewar et al. (2012) argues that a brief wakeful rest following new learning can boost memory for the learned material over short delays. To test this, participants learned a short story, followed immediately by either a 10 minute unrelated spot-the-difference task or a 10-minute wakeful rest interval. Retention was then assessed immediately, 15-30 minutes later, or after 7 days. The results indicated no difference in recall between groups immediately, but enhanced recall in the wakeful rest group in both the 15-30 minute and 7 day delay. This confirms that even a short period of wakeful rest following learning enhances recall across delays.

Additionally, Wamsley (2022) published a review claiming that the memory benefit of offline waking rest is comparable to the effect of post-learning sleep. It has been argued that common sleep paradigms impose a confound to the wake condition by forcing the participants to have their eyes open, are sitting, standing, or moving about in a lighted environment. When this is removed, it can be seen that short periods of unoccupied, task-free waking rest facilitate memory retention in much the same manner as sleep.

Sleep effects may face yet another challenge in future studies. To better understand the effect of sleep on memory, Mickes et al. (n.d.) conducted a series of experiments to demonstrate the importance of controlling for time of day. It has been proposed that time-of-day effects can pose as sleep benefits, when instead, performance is simply fluctuating throughout the day. Using an AM and PM control group, and examining the interactions between groups, avoids the time-of-day issue. For example, if memory performance is significantly better in the sleep group than the wake group, and memory performance is better for the AM control group than the PM control group, this could potentially reflect that testing time benefits memory, not necessarily a sleep benefit. In two experiments aimed to examine sleep's impact on memory, there was no evidence of a sleep benefit on memory and none of the data passed the critical interaction test. By using an AM-PM PM-AM interaction design that includes control groups, we can measure if memory performance is truly enhanced by a period of sleep.

Emotion, Memory, and Sleep

Many years of research have indicated that memories that evoke an emotional response are better remembered than memories that do not evoke an emotional response. Kensinger (2009) found that the extent to which an experience is physiologically arousing plays a role in the encoding, consolidation, and retrieval of a memory. When an experience elicits an arousal response, there are emotion-specific process at each of these stages. Arousing information is more likely to be attended, which increases the likelihood of the information being encoded (see also Laney et al., 2004). Once encoded, arousing information is more likely to be established into a durable memory (i.e., consolidated), and once stored, it is more likely to be retrieved than a neutral memory. Research has indicated that there is increased strength of connectivity between the amygdala and the hippocampus during the retrieval of emotional information, (Buchanan, 2007) which may lead to the enhanced ability to retrieve the details associated with an emotional experience.

While the arousal level of the stimuli is undoubtedly important for enhancing memory processes, valence also influences the likelihood that an event will be remembered. Negative events are often remembered with a greater sense of vividness than neutral information. For example, Costanzi et al. (2019) conducted four experiments examining the effect of incidentally encoded emotional stimuli on visuo-spatial working memory. To do so, rectangles were presented on the screen, followed by pictures that varied in emotional valence and arousal. Immediately after presentation, participants had to relocate the rectangles in the original position. On trials in which negative and neutral stimuli were presented, the results indicated that negative pictures were better relocated than neutral, independent of arousal. On trials in which valence (negative vs. neutral) was manipulated with arousal level (high vs. low), the results indicated that valence was significant, with negative valence having fewer displacement errors than neutral, whereas neither the effect of arousal nor the interaction were significant. The results from this study display the differential role of valence and arousal, and that under certain circumstances, valence can influence memory more that arousal. It has been proposed that there are two distinct routes to emotional memory; emotional memory enhancement for arousing information is dependent on an amygdalar-hippocampal network, whereas valenced, nonarousing information is supported by a prefrontal cortex-hippocampal network (Kensinger & Corkin, 2004).

There is a debate over the importance of sleep for preserving emotional memories, and indeed the research on it has produced mixed results across the existing literature. A widely accepted view of sleep and emotion is that during sleep, emotional memories are preferentially consolidated so that they are more readably accessible than neutral memories. This hypothesis has been tested myriad times in humans examining sleep after learning (e.g., Groch et al., 2013, Groch et al., 2015, Payne et al., 2008), and sleep deprivation (e.g., Wiesner et al., 2015), and nap studies (e.g., Nishida et al., 2008, Payne et al., 2015), all demonstrating a selective benefit of sleep for emotional memories. However, recent research has suggested that these effects might not be as robust as was once thought. For example, a recent meta-analysis indicated the differences in methodology such as timing and duration of the sleep conditions, type of waking control used, primary outcome measures, and age range studied, leads to difficulties accounting for discrepancy in results (Lipinska et al., 2019). A separate meta-analysis that examined sleep's impact on emotional memory suggests that sleep does not generally enhance emotional memory consolidation over neutral memory consolidation. The authors concluded that sleep's modulatory effects on emotional memory retention is rather complex and suggests that future research follow a structured set of methodological approaches, such as using similar recall and recognition tasks, study designs used to investigate sleep-related effects (e.g., sleep deprivation, nap sleep), task instructions, and similar stimulus materials (Schäfer et al., 2019; see also Cunningham et al., 2022).

One reason that findings differ between studies could be that different paradigms may be relying on different memory processes. Atienza and Cantero (2008) examined whether sleep and emotion interact to enhance declarative memory, or if they act independently of each other. For the study phase, participants learned 432 images varying in valence and arousal, from high to low arousal and negative and positive valence. Using a sleep deprivation paradigm, half of the participants were sleep deprived for 40 hours following the study phase while the other half slept normally at night following the study phase. For the testing phase, participants were presented with old and new images, and were asked to identify if the image was presented in the study phase using the remember (R) know (K) procedure. K is used when nothing can be recollected about the study occurrence, but the subject is confident that the picture had been previously studied. R is used when the participant recognizes that the picture has been studied and were consciously aware of specific details associated with the studied episode. In the dual process framework, K is also known as familiarity and R is known as recollection (Yonelinas, 2002). The results of this study indicate that sleep deprivation selectively impaired conscious remembering of qualitative information related to the study pictures (i.e., recollection). This demonstrates that the subjective experience of remembering and the underlying process of recollection were selectively impaired by the loss of sleep, whereas the subjective experience of knowing and the underlying familiarity process remained unaffected.

Pattern Separation

Pattern separation and pattern completion are functions of the hippocampus proposed to influence the encoding and retrieval of memories (Norman & O'Reilly, 2003). Pattern separation refers to the capability of the hippocampus to form nonoverlapping neural representations from similar stimulus inputs, whereas pattern completion refers to the process of transforming incomplete or degraded representations into previously stored representations by filling in the missing information (Stark et al., 2019). Behavioral, psychological, computational, and neuroimaging paradigms have evaluated the underlying processes of pattern separation and pattern completion (e.g., Ngo et al., 2020, Stark et al., 2010). Results from neuroimaging studies have shown that within the hippocampal system, CA1, CA3, and the denate gyrus are networks involved in pattern separation and pattern completion. Pattern separation is proposed to occur when the dentate gyrus produces nonoverlapping representations that are used by CA3 neurons during associative learning, which allows overlapping inputs to the hippocampus to be separated (Hunsaker & Kesner, 2013).

Pattern separation has commonly been measured in the mnemonic similarity task, (MST; see Stark et al., 2019 for a review) a recognition task that is highly sensitive to hippocampal function, placing strong demands on pattern separation processes. In this task participants are presented with pictures of everyday objects as an incidental encoding task during which they make indoor/outdoor judgments. Following this, the participants are presented with images from the study phase (targets), new images (foils) and images that are extremely similar to those seen during the study phase (lures). In one version of the test, participants identify each image as being old, similar, and new, indicating their ability to remember the details of the encoded images and their ability to keep similar lures and old items separate. Other versions of the test use just an “old” and “new” rating to obtain receiver operating characteristics (ROC).

The MST has been shown to measure differences in pattern separation across many variables. For example, Stark et al. (2013) examined age related changes in pattern separation performance. To do so, healthy adults with an age range of 20-89 years performed the MST, responding with “old”, “similar”, and “new” at test. The results demonstrated that pattern separation performance linearly declines with increasing age. The MST has also demonstrated differences in pattern separation when examining mild cognitive impairment and Alzheimer’s disease (e.g., Stark et al., 2013, Yassa et al., 2011, Ally et al., 2013), schizophrenia (Das et al., 2014), and aerobic exercise (Bernstein & McNally, 2019). Overall then, there is strong evidence that the MST is a good measure of pattern separation as carried out in the hippocampus (Stark et al., 2019).

Pattern Separation, Emotion, and Sleep

There also appears to be a relationship between pattern separation and emotional stimuli, though the results are not conclusive. For example, Leal et al. (2014) examined the effect of emotional modulation using the MST. The incidental encoding phase included negative, neutral, and positive images and the participants were instructed to rate the images on emotional valence. They were then given a subsequent recognition test 5 minutes after the encoding phase or 24 hours later in which they were presented with lure, target, and foil items. The participants were asked to indicate whether these images were “old” or “new.” They found that lure discrimination was diminished for emotional compared to neutral stimuli. This indicates the possibility that participants may not have perceptually encoded all of the details of the emotional images, and this lack of attention to detail may have affected subsequent memory performance. The authors suggest that emotion results in a preservation of gist information and a loss of detail information (see also Sharot & Yonelinas, 2008).

Leal et al. (2014) also examined emotional modulation of memory at the level of hippocampal subfields. They observed the engagement of hippocampal DG/CA3 during accurate discrimination of similar items, meaning there is an involvement of the hippocampal network during the pattern separation of emotional stimuli. They also found that there was an emotional modulation specific to trials in which participants accurately discriminated similar emotional items, indicating that the DG/CA3 uses emotional information to discriminate similar inputs.

More recently, Szollosi and Racsmany (2020) investigated whether emotionally arousing memories are more distinct as compared to neutral memories. Using a version of the MST that included old, new, and similar responses, the results indicated that individuals were better in discriminating between similar, emotionally arousing memories when compared to the neutral stimuli. This finding contradicts the claims made by Leal et al. (2014), but the authors state that this difference may be due to having different dependent variables to index lure discrimination.

The relationship between sleep and pattern separation has not received much attention. Across the literature, it has been hypothesized that during sleep, hippocampal reactivation is related to the processes of pattern separation such that there are measurable behavioral differences on tasks of pattern separation following a manipulation of sleep. Hanert et al. (2017)

used the MST to study how sleep affects hippocampal representations by enhancing and/or diminishing pattern separation. To do so, participants encoded pictures of objects and performed an immediate recognition test. Then, after a 9-hour retention interval of either sleep or daytime wakefulness, participants performed another recognition task. The results indicated that pattern separation deteriorated after a wake period but remained stable across sleep. Likewise, Doxey et al. (2018) found that there was a decrease in mnemonic discrimination following a wake-filled delay but there was preserved performance when the delay contained sleep. Thus, initial research suggests that there is a sleep-related benefit that can be attributed to the stabilization of pattern separation, but this research is not without its criticism. For instance, Poh and Cousins (2018) argued that reduced scores on pattern separation might be driven by greater forgetting in the wake group rather than stabilization in the sleep group, and that future experimentation is required to examine whether sleep does indeed stabilize pattern separation in the hippocampus.

Current Study

There is a noticeable lack of sufficient evidence regarding the effects of sleep and emotion on pattern separation. Only three studies have looked at emotion and pattern separation, and another two examined sleep and pattern separation. Additionally, recent meta-analyses have raised questions about the preferential consolidation of emotional memories, and failures to find a sleep effect have posed a challenge to the consensus that sleep affects memory in general. To address these issues, the current study investigated the influence of sleep on the consolidation of emotional and neutral memories in a pattern separation task. Measures of item recognition, pattern separation, and recollection and familiarity were collected. Pattern separation was measured by using the Lure Discrimination Index (LDI) of the MST, which is the difference between the rate of “old” responses to lure items and old items. The dual process signal detection (DPSD) model (e.g., Yonelinas, 1994) was used to obtain estimates of recollection and familiarity from item recognition. Recollection is defined as the retrieval of qualitative information about a specific study episode, whereas familiarity is a global measure of memory strength or stimulus recency (Yonelinas, 2002).

In order to examine the effect of sleep and emotion on pattern separation, participants performed the MST. The “sleep effect” was defined as the interaction between time of encoding (morning or evening) and time of retrieval (morning or evening) (Mickes et al., n.d.). Given that the bulk of the research has found sleep effects on memory, we expected an effect of sleep on pattern separation, showing that participants discriminate the images better after sleep than the wake and control groups. If previous reports of a preferential effect of sleep on emotional memories hold true, the sleep effect would be larger for emotional stimuli than for neutral stimuli. However, finding a null effect of sleep on emotional vs. neutral memory would support the recent meta-analyses and finding a null sleep effect would support recent research in the field.

Chapter 2: Methods

Participants

A total of 102 participants between the ages of 18-35 (M = 20.5 SD = 3.26, 66% female) were included in the data analyses. Participants included undergraduate students at the University of Nevada, Las Vegas and Las Vegas community members. Participants received either credit towards their introduction to psychology course research requirement or monetary compensation. A power analysis using G*Power (Version 3.1.9.6) indicated that we needed 92 participants in order to achieve 90% power to detect an interaction with an effect size of partial eta squared = .04. We rounded up to 96 in order to fulfill our counterbalance conditions.

Materials

We compiled 760 negative and neutral images to perform a norming study. One independent group of participants viewed all of the negative and neutral images and rated the valence and arousal level of each item on a scales of 1 to 9 (1 being the most negative and the least arousing respectively, 9 being the most positive and the most arousing respectively). Another independent group of participants viewed all of the lure and target images and rated the set of images on similarity on a scale of 1-9 (1 being the least similar, 9 being the most similar). We analyzed the valence, arousal, and similarity ratings to construct the MST that was used during the experiment. We chose the pictures by selecting 240 of the most negatively ranked (M = 1.76, SD = .276), and 240 neutrally ranked pictures (M = 4.9, SD = .45). We then made sure that the negative and neutral lure images were rated as highly similar (M = 6.5, SD = .84, M = 6.3, SD = .78, respectively). We did not consider arousal levels while choosing our images since we were primarily interested in valence levels.

The MST consisted of an incidental encoding phase and a recognition task. The incidental encoding phase of the MST consisted of 240 images, 120 negative and 120 neutral. The recognition task consisted of old images that were seen during the incidental encoding phase, new images, and images that are extremely similar to those seen during the incidental encoding phase (lures). The recognition task consisted of 120 old images, 60 negative and 60 neutral images, and an additional 240 new images consisting of 60 new neutral, 60 new negative, 60 neutral similar lures, and 60 negative similar lures. Six counterbalance orders were used to display the old, similar, and lure images in each condition equally often across subjects.

Procedure

Participants were randomly assigned to one of four groups: sleep, wake, AM control, or PM control. The task consisted of two sessions, with either a 1-hour or 12-hour retention interval. After a participant signed up for the study, they were then emailed with a consent form and the Pittsburgh Sleep Quality Index (PSQI). They filled both forms out and the results from the PSQI were evaluated to ensure that the participants did not display any abnormal sleep habits. An abnormal sleep schedule was indicated by scoring above a 6 on the PSQI. Once deemed eligible, participants completed session one, where they came to the lab and performed the incidental encoding phase of the MST. Participants in the wake and AM control group came to the lab at 9am and participants in the sleep and PM control came to the lab at 9pm. Participants viewed a series of 120 negative and 120 neutral images (using E-Prime 3.0). For each image, participants made valence judgements by rating the image on a scale of 1-3 using the computer keyboard (1 being negative, 2 being neutral, and 3 being positive). Each image was presented for 1500ms with a 500ms interstimulus interval. The task would move to the next image if participants did not respond with their valence rating during the time window.

For session 2, participants came back to the lab and performed the self-paced recognition task. The recognition task took place 12-hours after the incidental encoding phase for the sleep and wake groups, and 1-hour after the incidental encoding phase for the AM and PM control groups. Participants were asked to refrain from caffeine and alcohol during both sessions, and to refrain from napping in the wake group.

For each image, participants identified it as being “old” or “new”. Images that the participant thought were similar were called “new”. Since the lure images are very similar to the studied images, participants were given explicit instructions and an example on what exactly a similar lure was and how to identify whether these images are “old” or “new”. Participants were asked to rate their confidence in identifying whether the images are “old” or “new” on a rating scale from 1-6 (1 being sure new, 6 being sure old). After participants completed the recognition task, they filled out a strategy sheet and the Morning-Eveningness Chronotype form.

Chapter 3: Results

Analyses

Measures of pattern separation and item recognition were taken from the MST. Pattern separation was measured as the difference between the rate of old responses to lure items and to old items. Item recognition was measured as the ability to discriminate between old items and new items. The assessment of the effects of sleep was based on better discrimination following a period of sleep than wake.

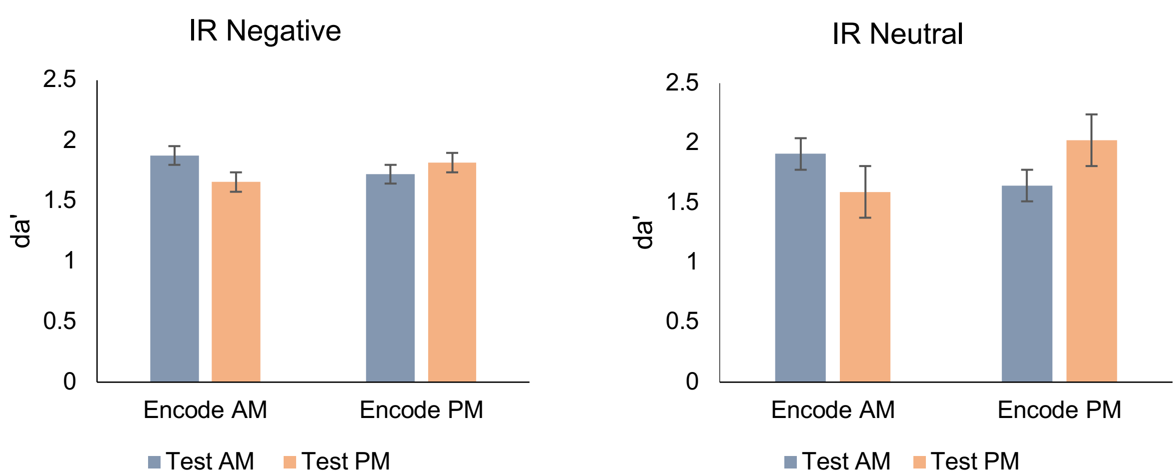
Bayesian ANOVA's were conducted comparing encoding time, test time, and emotion for both pattern separation and item recognition. Bayesian independent-sample t-tests were conducted to examine differences between the sleep and wake group for both pattern separation and item recognition. Bayes factors were interpreted based on evidence categories from Wetzels et al. (2011) and are as follows: BF = 1, no evidence; 1-3, anecdotal evidence for H_A; 3-10, substantial evidence for H_A; 10-30, strong evidence for H_A; 30-100, very strong evidence for H_A; >100, decisive evidence for H_A.

Confidence ratings were used to calculate estimates of recollection and familiarity through the dual process signal detection (DPSD) model. Recollection and familiarity were collected from measures of item recognition and pattern separation.

Item Recognition

Results from the three-way mixed Bayesian ANOVA comparing encoding time, test time, and emotion (the within-subjects factor) for item recognition produced strong evidence of a null effect for the interaction (BF_{10} = .004). There was also a null effect of encoding time (BF_{10} = .202), test time (BF_{10} = .200), and emotion (BF_{10} = .154). In line with our preregistration, we then performed two two-way between-subjects Bayesian ANOVAs to determine if there was a sleep effect for negative and neutral images separately. The results showed evidence of a null interaction effect between encoding and test time for both negative images (BF_{10} = .128) and neutral images (BF_{10} = .097). Bayesian independent sample t-tests for the sleep and wake groups also showed evidence for a null effect for the negative (BF_{10} = .299) and neutral images (BF_{10} = .291). Thus, the sleep and wake group did not differ significantly for negative or neutral images (Figure 1).

Figure 1. *Item Recognition (IR) for Negative and Neutral Images*

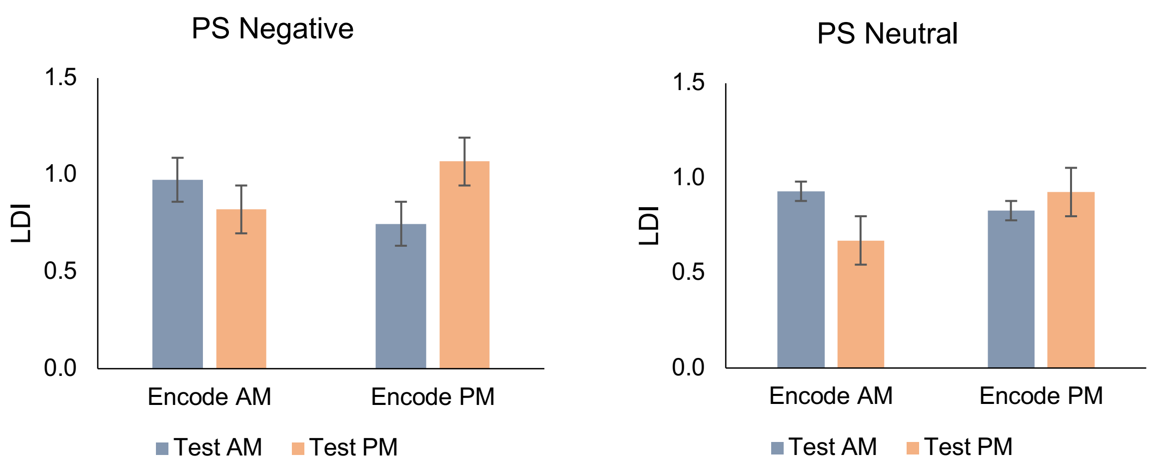


Note. The graphs above show item recognition measured in d_a across the four groups, with negative images on the left and neutral images on the right. Both graphs depict null effects. Bars are one standard error of the mean.

Pattern Separation

A three-way Bayesian ANOVA was conducted for pattern separation (measured as the difference between the rate of old responses to old items and to lure items). The interaction between emotion, encoding time, and test time revealed strong evidence of a null effect (BF_{10} = .006). Further, the results showed a null effect of encoding time (BF_{10} = .234) and test time (BF_{10} = .226). The two two-way Bayesian ANOVAs also showed evidence for null interaction effects between encoding and test time for negative (BF_{10} = .089) and neutral images (BF_{10} = .103). Bayesian independent samples t-test directly comparing the sleep and wake groups within each emotion condition showed anecdotal evidence for a null effect for the negative (BF_{10} = .351) and no evidence either way for the neutral images (BF_{10} = .856). Thus, the sleep and wake group did not differ significantly for negative or neutral images (Figure 2).

Figure 2. *Pattern Separation (PS) for Negative and Neutral Images*

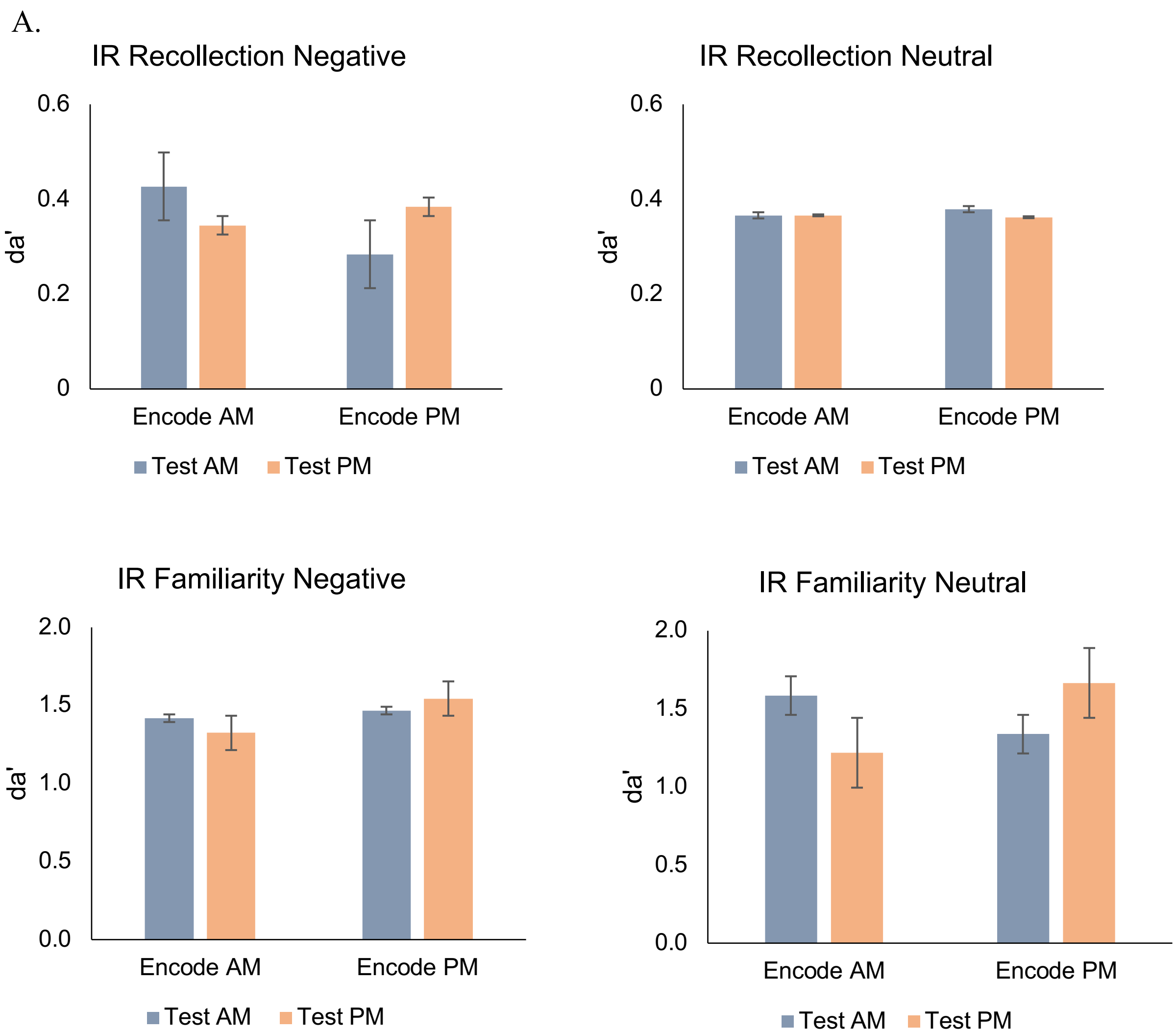


Note. The graphs above show pattern separation measured using the Lure Discrimination Index (LDI) across the four groups, with negative images on the left and neutral images on the right. Both graphs depict null effects. Bars reflect one standard error of the mean. PS = Pattern separation.

Item Recognition: Recollection and Familiarity

Bayesian ANOVAs were conducted comparing encoding time, test time, and emotion for recollection and familiarity measured from the item recognition test. Results for recollection showed a null effect of the interaction (BF_{10} = .056) and the main effects of encoding time (BF_{10} = .272) and test time (BF_{10} = .205). Results for familiarity showed a null effect of the interaction (BF_{10} = .103), anecdotal evidence for a null effect of encoding time (BF_{10} = .375) and a null effect of test time (BF_{10} = .275). This indicates that sleep and emotion had no effect on the recollection and familiarity processes.

Figure 3. *Recollection and Familiarity Estimates for Item Recognition (IR) for both Negative and Neutral Images*



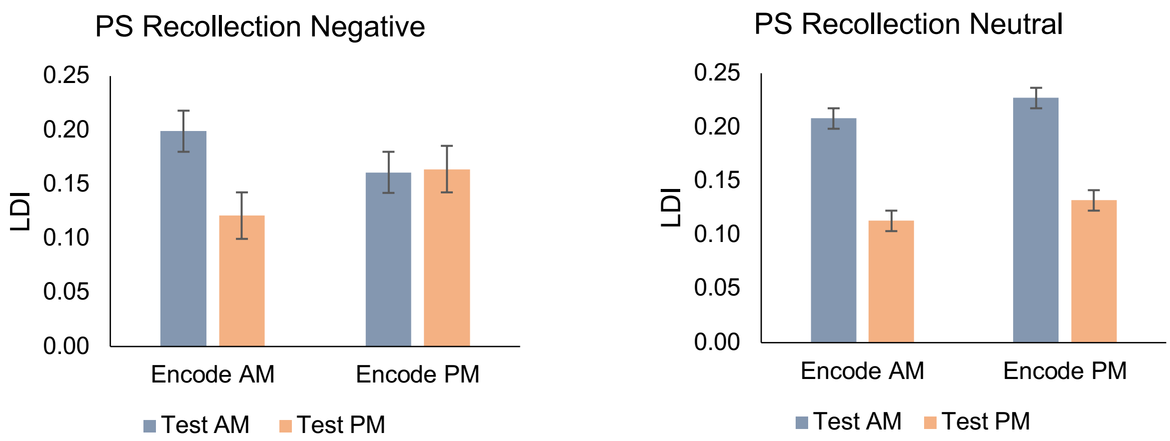
Note. The graphs above show recollection (A) and familiarity (B) estimates for item recognition across the four groups, with negative images on the left and neutral images on the right. All graphs depict null effects. Bars reflect one standard error of the mean.

Pattern Separation: Recollection and Familiarity

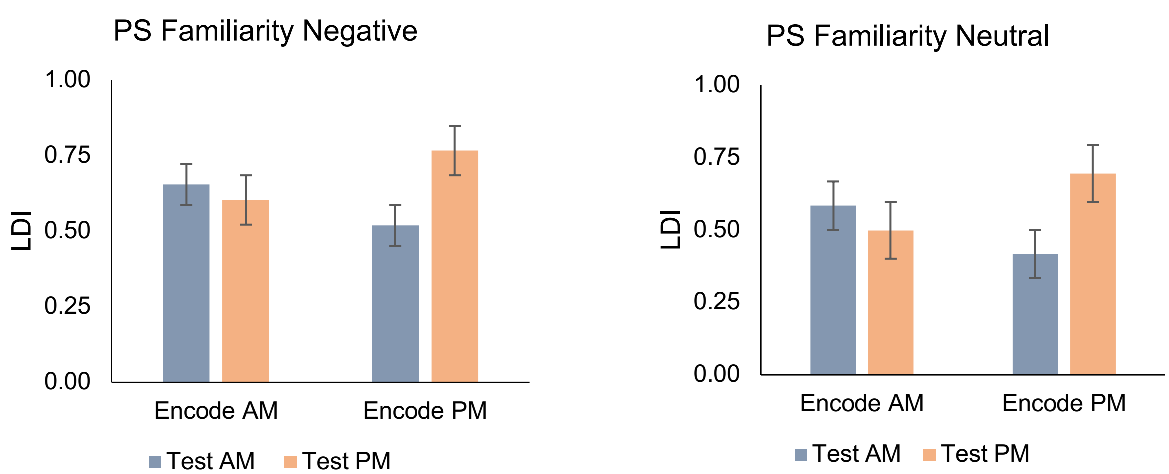
Bayesian ANOVAs were conducted for recollection and familiarity as measured from pattern separation performance, comparing encoding time, test time, and emotion. Results for recollection showed weak evidence for a null effect of the interaction (BF_{10} = .412), weak evidence for an effect of test time (BF_{10} = 1.389) and good evidence for a null effect of encoding time (BF_{10} = .243). For familiarity, there was anecdotal evidence for a null effect of test time (BF_{10} = .698) and evidence for a null effect of encoding time (BF_{10} = .244). Overall, the results showed no effects of emotion or study/test time conditions.

Figure 4. *Recollection and Familiarity Estimates for Pattern Separation (PS) for both Negative and Neutral Images*

A.



B.



Note. The graphs above show recollection (A) and familiarity (B) estimates for pattern separation across the four groups, with negative images on the left and neutral images on the right. All graphs depict null effects. Bars reflect one standard error of the mean.

Chronotype Score

To use assess chronotype, the Morning-Eveningness questionnaire was used. Participants could score one of five chronotypes: definite morning (N = 0), moderate morning (N = 14), intermediate, (N = 78), moderate evening (N = 7), and definite evening (N = 2). A 4x4 Pearson chi-square test was performed to examine whether there were group differences in chronotype. The findings showed that chronotype did not differ between groups, $X^2 = 9.185$, $p = .687$.

Chapter 4: Discussion

The purpose of the current study was to determine if a period of sleep enhanced memory for emotional images more than a period of wake. This study was sparked by the recent controversy regarding sleep, emotion, and memory, with the intent of providing clarity to the mixed results. We chose to incorporate pattern separation as a new measure because it targets the underlying hippocampal mechanisms that occur during a period of sleep.

Overall, the results did not support the proposed hypotheses. The main findings of the reported study are: 1) the sleep group did not perform better on measures of pattern separation or item recognition; and 2) there was no preferential consolidation of emotional images over neutral images. Surprisingly, we also found null effects of emotion on all memory measures.

While the results did not support our hypotheses, they add more clarity to the controversy concerning the sleep and memory literature. Finding no difference between the sleep and wake groups is in line with claims made by Siegel (2021) and Wamsley (2022) that memory consolidation can occur during periods of offline wake. It might be that there is a memory benefit of offline waking rest that is comparable to post-learning sleep. This is an increasingly popular theory that posits that even a brief period of eyes-closed rest can lead to the same behavioral effect as sleep, and further, that there are several common neurobiological features of sleep and waking rest. These include a reduced level of acetylcholine and sensory processing, and the emergence of memory reactivation during hippocampal sharp-wave ripples (Wamsley, 2022).

If offline consolidation is not driving better memory after sleep, then what is? Myriad papers have demonstrated that a quiet waking period or meditative waking state produces a gain in memory performance similar to that seen in sleep, relative to an active waking state or sleep deprived state (Siegel, 2021). For example, Brokaw et al. (2016) demonstrated that a short period of quiet rest can facilitate memory, and that this may occur via an active process of consolidation supported by slow oscillatory EEG activity. Participants listened to a short story, either rested for 15 minutes or performed a 15 minute distractor task, and then performed a recall test. The results showed an increase in slow oscillatory EEG rhythms and decrease in alpha rhythms, both predicting improved memory following rest. These results, as well as others (see also Mercer, 2015, and Humiston, 2016)., suggest that periods of quiet rest are critical for consolidation, and future research should be performed to understand this better.

Across all groups, there was no effect of emotion. The longstanding view on sleep and emotion is that emotional memories are preferentially consolidated during sleep, whereas neutral memories tend to become less accessible. However, this view has been challenged recently by two metanalyses. Lipinska et al. (2019) claim that there are no conclusive results across the literature that demonstrate that sleep preferentially consolidates emotional over neutral memories. Similarly, Schafer et al. (2019) argued that the results from their meta-analysis do not support the hypothesis that sleep enhances emotional memory beyond the typical effect of emotion on memory.

Although emotion typically affects recognition memory, we found no effects on either item recognition or pattern separation. One potential explanation for why the negative images were not better remembered than the neutral images was the overall memorability of all the images. Memorability accounts for how perceptual processes select stimuli for encoding and later for retrieval (Bainbridge, 2017). Memorability automatically tags the statistical distinctiveness of stimuli for later encoding, and has been conceptualized as an intrinsic, measurable property of a stimulus, that is different from attention, cognitive control, and priming (Bainbridge, 2019).

There are several attributes that contribute to this feature of stimuli, and explain why some images are more memorable than others. For example, scene images with faces or text tend to be memorable, as well as abstract visualizations such as graphs, figures, and infographics (Bainbridge, 2019). However, the number of objects or image coverage by objects in a scene is not related to the overall scene's memorability. Along with that, aesthetics, such as how interesting a scene is, is not correlated with memorability. While various work has suggested that memorability is consistent across people, it is not entirely clear what makes a stimulus memorable, though machine learning can make specific predictions about what people will remember or forget (Needell & Bainbridge, 2021). Although we have no measure of memorability for our stimuli, this may provide an explanation of why the mundane, neutral images were remembered as well as the emotion-inducing negative images; specifically, they may have been equal or greater in memorability, thereby countering effects of emotion. Further tests with these stimuli would be needed to provide support for that possibility.

Our results showed no difference of lure discrimination between the sleep and wake groups. Previous literature found that pattern separation was stabilized after a period of sleep, but diminished after wakefulness (Hanert et al., 2017, Doxey et al., 2018). Research examining sleep and pattern separation is relatively new, though there are critiques of this research. For example, Poh & Cousins (2018) argue that the sleep effect seen in Hanert et al. (2017) cannot truly be attributed to stabilization of pattern separation. Instead, the reduced scores on pattern separation might be driven by greater forgetting in groups that remain awake after encoding. In our study, it could have been that memory retention was initially higher in the wake group than the sleep, but 9 hours of daytime wakefulness resulted in forgetting that reflected no difference in pattern separation between the groups at test. Future studies could examine this by using an immediate recall test to examine baseline performance among participants.

In our study, there was no effect of emotion pattern separation, and there are mixed results between the two studies that have examined this. Leal et al. (2014) found enhanced discrimination for neutral images, whereas Szollosi and Racsmany (2020) found negative images yielded enhanced discrimination. While we did not predict which valence would result in higher discrimination (due to this discrepancy), we saw no difference between the negative and neutral images.

Chapter 5: Limitations and Future Directions

Our examination of sleep and memory showed no behavioral evidence of an effect of sleep on memory, although we did not have access to equipment to record sleep physiology, which would provide measures of time spent in each stage of sleep, amongst other things. After the study, we asked participants to report the time they slept the night before session 2. The average was 7.38 hours (N = 92, 10 participants' data was missing). Though we had this subjective measure, we had no real control over when participants went to bed or woke up prior to the experiment. Future experiments could include an objective measure of sleep, and further, compare sleep stages to see if there is a physiological relationship between time spent in slow wave sleep or REM and memory the following morning.

We did not use positive images in our study. This could have been a limitation, for it has been demonstrated that studies elicit a stronger emotional effect when they combine negative and positive images as their emotional condition and compare that to neutral images (van den Hout et al., 2014). Past research has shown that when testing memory for the three emotional categories – negative, positive, and neutral – positive and negative stimuli are often associated with superior retention levels relative to the neutral condition (van der Helm & Walker, 2011). We wanted to elicit an emotional response only by using negative images, to better understand how sleep and emotional memory are related, though we may have dampened this effect by not including positive images in our study.

Another potential limitation in this study was that the negative images were too negative, to the point where participants did not encode them properly. To examine this, a post-hoc repeated measures ANOVA was conducted to examine the difference between reaction times for images presented during the encoding phase. It should be noted that we included a positive valence rating during the encoding phase, though we did not include positive images that had been normed as positive in the study. We used a scale with positive ratings on it anyway so that participants were not aware that there were no positive images being used.

The results indicated a significant difference between reaction times for the negative, neutral, and positive ratings, $F(1, 98) = 55.938$, $p < .001$, $\eta^2 = .363$). To better understand this, paired sample t-tests were conducted. Reaction times for negative images were significantly faster than for neutral, $t_{101} = -7.329$, $p < .001$, $d = -.726$, and for positive $t_{101} = -7.2517$, $p < .001$, $d = -.752$. Reaction times for ratings of negative images ($M = 830.510$ms, $SD = 123.774$) were 125.6716ms quicker than ratings for neutrally rated images ($M = 956.181$ms, $SD = 144.823$); 95% CI[-159.6861, -91.6570]) and 163.1618ms quicker than ratings for positively rated images ($M = 993.672$ms, $SD = 189.663$; 95% CI[-205.7569, -120.5666]). It is possible that the negatively rated images may have elicited an emotional effect if they were given the same encoding time as neutrally and positively rated pictures. Future studies could examine this by using an extended presentation duration of the images during the encoding phase. This may require changing the negative stimuli to be less negative.

Chapter 6: Conclusion

Research examining sleep and emotional memories has led to increasingly mixed results. This study aimed to disentangle those results, with the intent of providing more clarity to the literature. The results showed no difference between the sleep and wake group on measures of pattern separation or item recognition and no preferential consolidation of emotional images over neutral images. Although our conclusions must be treated with caution due to limitations of the study, these data do suggest that a period of sleep is not more beneficial for the consolidation of emotional memories than a period of daytime wakefulness. Future research is certainly needed to further understand the relationship (or lack thereof) between sleep and memory.

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