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The Effect of Sleep-Dependent Consolidation on Pattern Separation and Pattern Completion in Delayed Retrieval

Jesse Ray James
Brigham Young University - Provo

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The Effect of Sleep-Dependent Memory Consolidation on Pattern Separation and

Pattern Completion in Delayed Retrieval

Jesse Ray James

A dissertation submitted to the faculty of
Brigham Young University
in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

C. Brock Kirwan, Chair
Erin D. Bigler
Scott A. Baldwin
Shawn D. Gale
Harold L. Miller

Department of Psychology

Brigham Young University

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ABSTRACT

The Effect of Sleep-Dependent Memory Consolidation on Pattern Separation and
Pattern Completion in Delayed Retrieval

Jesse Ray James
Department of Psychology, BYU
Doctor of Philosophy

While people sleep, the brain replays the same neural firings that resulted from waking activities that day. This results in greater memory strength following a sleeping delay than a waking delay. The current project built upon this fact in a series of three experiments.

Experiment 1. Although previous research has demonstrated a benefit of sleep to memory strength, the literature has not established the impact of sleep on memory specificity. Computational models of medial temporal lobe function posit that discrimination and generalization across similar memories are accomplished through processes known as pattern separation and pattern completion, respectively. To discover whether sleep predisposes people toward pattern separation or pattern completion, participants studied pictures of common objects. After a 12-hour delay, during which participants either slept or stayed awake, participants indicated whether "lure" images were exactly the same or merely similar to those they studied. There was better memory discrimination in those who slept, consistent with a bias toward pattern separation following sleep.

Experiment 2. In order to discover whether the pattern of memory demonstrated in Experiment 1 would carry over to semantic memories, participants studied textbook material and took a true/false test 12 hours later. There was a shift in the response trends following sleep, such that participants were more likely to mistakenly endorse highly similar false statements as "true" but were also more likely to correctly endorse more dissimilar false statements as "false." However, we did not detect evidence of an increased bias toward pattern separation or pattern completion following sleep for this material. Our findings appear consistent with the prediction that memory specificity is benefitted by sleep.

Experiment 3. Previous research has demonstrated that memories encoded later in the day are consolidated better than memories encoded earlier in the day. However, these studies have not controlled for the differential decay that memories suffer across these two elapsed periods. In this study, we attempted to show the degree of improvement afforded by sleep using a before-sleep comparison group. However, post hoc analyses revealed a significant interaction between the proposed outcomes and whether participants had napped during the day. These preliminary findings may suggest that napping differentially affects the consolidation of information studied before and after napping.

Keywords: memory, sleep, consolidation, pattern separation, pattern completion

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When I applied to the doctoral program in psychology at BYU, I never really expected to get in. And when I did, I was afraid they'd soon discover their mistake and kick me out. Thankfully, my experience at BYU has been the antithesis of those expectations. I have been made to feel competent and capable and I find myself grateful to the institution for establishing such an enriching culture. In my time here, I have grown intellectually, emotionally, and spiritually. I love my professors—in particular, my mentor, Brock Kirwan, who has been more wonderful than I could possibly have imagined. He has been supportive and flexible and encouraging. He is an engaging teacher, a clever researcher, a charming person, and he has come to be a good friend.

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Chapter 1: Literature Review

Declarative memory is the ability to encode, store, and retrieve mental representations of any number of stimuli that can be verbally described (Eichenbaum, 1997). Declarative memories may include mental representations of faces, objects, words and discourse, music, semantic facts, and autobiographical events. The hippocampus and adjacent cortex, known together as the medial temporal lobe (MTL), support declarative memory (Eichenbaum, 2004; Norman, Detre, & Polyn, 2008; Squire, 1992). The primary tasks of the MTL are spatial navigation, pattern recognition, and the long-term consolidation of declarative memories (Best, 1998).

A Model of Memory

Computational models of MTL function, such as the complementary learning systems (CLS) model, suggest that the hippocampus is especially enabled to rapidly encode new declarative-memory representations (Norman et al., 2008; Norman & O'Reilly, 2003). These hippocampal mechanisms, which allow for the rapid creation of labile representations, are complemented by neocortical mechanisms that allow for the gradual creation of relatively more stable representations (O'Reilly & Rudy, 2001).

The CLS model suggests that, during sleep, the hippocampus replays waking neuronal activity to consolidate its representations (Norman, Newman, & Perotte, 2005). Consolidation is defined as the strengthening of newly-formed memories and is achieved by integrating the representations into related neural networks (Diekelmann, Wilhelm, & Born, 2009). Specifically, consolidation via hippocampal replay functions to gradually transfer the storage site of memory representations from the hippocampus to the association cortex. By storing a representation in the cortex, the brain is figuratively filing the memory in a network of other,

related memories (Alvarez & Squire, 1994), resulting in more generalized, stable, and useful—but less specific—memories than existed prior to sleep.

Studies performed to test the CLS model support the notion that the hippocampal and neocortical learning systems function in a complementary way in order to discriminate between some memories and generalize across others, depending on the context during encoding and retrieval (Duncan, Sadanand, & Davachi, 2012; Holdstock et al., 2002). The mental computation that gives rise to this generalization across stimuli is known as pattern completion; it occurs when a stored representation is retrieved in response to a partial, degraded, or related cue (Stark, Yassa, & Stark, 2011). Alternatively, the computation underlying perceptual discrimination is known as pattern separation. Pattern separation occurs when two related stimuli are stored as distinct representations (Bakker, Kirwan, Miller, & Stark, 2008), and, in its most technical sense, is alleged to occur when output firing patterns of hippocampal networks corresponding to a given stimulus are more dissimilar than their respective input firing patterns (Deng, Aimone, & Gage, 2010). Thus, whereas pattern completion only occurs during the retrieval of a memory, pattern separation occurs during the memory's encoding (Deng et al., 2010).

In most individuals, these two processes are executed in balanced fashion as the brain attends to incoming stimuli. In other words, the hippocampus engages in both processes concomitantly, but because the relative benefit of pattern separation and pattern completion depends on the situation, behavioral responses will often reflect the more adaptive of these two processes, given the cognitive demands of the task at hand. Pattern completion, for instance, would allow an individual to sustain a motor routine despite minor anomalies, whereas pattern separation would allow him or her to identify major anomalies. To illustrate the point, consider an employee of a large corporation. Pattern completion would allow this person, at the end of a

typical day, to find her car parked in the lot in which she usually parks, despite minor deviations in the precise location of the car from day to day. Alternatively, she might arrive late, to find the parking lot full and so parks in an entirely different lot. Pattern separation would allow her to discriminate this day's unique events from other parking-lot memories so that she can find her car at the end of the day without mistaking the wrong lot.

Harmony between pattern completion and pattern separation ensures normal memory functioning. In fact, Sahay, Wilson, and Hen (2011) suggested that psychological disorders may result from bias toward one process or the other. For instance, a bias toward pattern separation ultimately can result in the excessive attention to details noted in autism, obsessive compulsive disorder, etc., whereas a bias toward pattern completion can result in excessive generalization as observed in anxiety, depression, and post-traumatic stress disorder (Sahay et al., 2011).

Memory Consolidation During Sleep

Performance on declarative and procedural memory tasks is often better following sleep than following similar delay periods in which no sleep occurred (Diekelmann et al., 2009). Early sleep studies concluded that this was likely because a sleeping individual escaped interference that occurred during waking activity (Jenkins & Dallenbach, 1924). However, later research has suggested that this account is incomplete. For instance, Gaab and colleagues (Gaab, Paetzold, Becker, Walker, & Schlaug, 2004) demonstrated that the amount of interference during waking does not differentially impact memory retention post sleep. In their study, memory for auditorily-presented information was improved by sleep regardless of whether the material was learned in the morning (i.e., a long delay before sleep) or in the night (i.e., a short delay before sleep), suggesting that, in addition to protecting memories from further interference, sleep must further bolster memory representations in some fashion. Furthermore, mere isolation from

interference by waking activity prior to sleep cannot account for the fact that memories are also more resistant to interference that occurs following sleep (Diekelmann et al., 2009).

The stabilizing of memories (i.e., actively retaining them, making them impervious to decay) and the enhancement of memories (i.e., improving and strengthening them beyond mere maintenance) are both referred to as consolidation in the relevant literature (see, e.g., Walker & Stickgold, 2004). It appears, however, that, whereas memory enhancement absent intentional rehearsal occurs only during sleep, memory stabilization may occur during wakefulness or sleep (Muellbacher et al., 2002). A plausible explanation for this disparity may be that the conscious mental processing that recurs during wakefulness precludes neural networks from reprocessing and consolidating the information into long-term memory until consciousness is forfeited during sleep (McClelland, McNaughton, & O'Reilly, 1995).

Sleep-dependent consolidation has been shown to enhance both declarative and non-declarative memories (Diekelmann et al., 2009). Declarative memories appear to benefit equally from as little as 1-2 hrs of sleep as from an entire night's sleep (Diekelmann et al., 2009). For this reason, daytime naps may be beneficial in consolidating declarative memories. For instance, naps have been shown to restore performance decrements caused by repeated practice and to improve performance on visual perception tasks as much as a full night's sleep does (Mednick et al., 2002; Mednick, Nakayama, & Stickgold, 2003). On the other hand, sleep's benefit to procedural memories appears to be dose-dependent (Diekelmann et al., 2009), and, although procedural memories can be stabilized in about 6 hrs without sleep, they are only enhanced with sleep (Walker, Brakefield, Hobson, & Stickgold, 2003).

Physiology of Sleep

Sleep can be separated into two main components: Rapid eye movement (REM) sleep

and non-REM sleep. REM sleep also has been termed paradoxical sleep because it is

characterized in the electroencephalographic (EEG) record by the presence of strong beta (13-30

Hz) activity—similar to brain activity in a waking state (Rechtschaffen & Kales, 1968).

Alternatively, the EEG output during non-REM sleep is characterized by slower waves than the

alpha (7-13 Hz) and beta waves of a waking state, and is further divided into three or four stages

of increasing depth (Rechtschaffen & Kales, 1968). The first stage of non-REM sleep is

inconsequential to memory; it is merely a transition from wakefulness to deeper sleep. Stages 2,

3, and 4, however, appear to be integral to memory consolidation, but the specific contribution of

each stage remains unclear. Some researchers claim that stage-2 sleep is responsible for the

consolidation of both declarative (Genzel, Dresler, Wehrle, Grozinger, & Steiger, 2008) and non-

declarative memories (Smith & MacNeill, 1994; Walker et al., 2003; Walker, Liston, Hobson, &

Stickgold, 2002). Others claim that stages 3 and 4 are responsible for the consolidation of

declarative memories, and that REM sleep is responsible for the consolidation of non-declarative

memories (Fischer, Hallschmid, Elsner, & Born, 2002; Plihal & Born, 1997). One possible

reason for the disparate views may be that previous studies have failed to control for the

confounding interweaving of stage-2 sleep that spontaneously occurs throughout what would

otherwise be longer, uninterrupted blocks of REM and stage-3 and -4 sleep.

Non-REM sleep. On average, more time is spent in stage 2 sleep than in any other, and

time spent in this stage appears to be evenly distributed throughout the night (Plihal & Born,

1997). This stage of sleep is characterized by increased theta activity (4-7 Hz). Sleep stages 3

and 4 are marked in the EEG record by low-frequency delta waves (0-4 Hz) and are thus together

termed slow-wave sleep (SWS). The slow waves in stages 3 and 4 reflect underlying cortical synchrony, suggesting that large neuronal networks are firing together in waves (Amzica & Steriade, 1995). The bulk of SWS occurs during the first half of the night. A critical component of non-REM sleep stages 2, 3, and 4 is the presence of sleep spindles (7-14 Hz) in the EEG record. Sleep spindles originate in the neocortex and are immediately preceded by sharp ripples (200 Hz) in the hippocampal waves (Siapas & Wilson, 1998). These combined ripple/spindle events are the theorized mechanism for memory consolidation (Wilhelm et al., 2011). Hippocampal ripples are detected by deep-brain electrodes in rodents and reflect the firing of interneurons followed by that of pyramidal cells in the hippocampus (Le Van Quyen et al., 2008). During each hippocampal ripple, the same neural networks that were activated during waking tasks are reactivated (Plihal & Born, 1997). For instance, the firing patterns of hippocampal place cells in a rat's brain are repeated during sleep exactly as they fired when the animal was performing a waking task (Wilson & McNaughton, 1994). Often, but not always, this recapitulation of waking brain activity occurs with significantly more rapidity during sleep than during the inceptive encoding (Louie & Wilson, 2001; Poe, Nitz, McNaughton, & Barnes, 2000; Ribeiro et al., 2002; Skaggs & McNaughton, 1996).

Selective experimental suppression of hippocampal ripples in the rat brain during sleep inhibits the retention of spatial memories, suggesting that the ripples, and their resultant cortical spindles, are the primary mechanisms for memory consolidation (Ego-Stengel & Wilson, 2010; Girardeau, Benchenane, Wiener, Buzsaki, & Zugaro, 2009). In humans, the spindle density in the typical EEG record is about six spindles per min, with an increase of as much as 33% when a new task is being learned (Gais, Molle, Helms, & Born, 2002). This suggests that daytime experiences conceivably may be replayed thousands of times each night.

Interestingly, consolidation can be experimentally induced by pairing odors with performance on a task. Later presentation of those same odors during non-REM sleep cues hippocampal ripples, thereby improving consolidation, as evidenced by subsequent task performance (Rasch, Buchel, Gais, & Born, 2007). Other, naturally-occurring factors can influence the amount of sleep-dependent replay as well. For instance, memories are benefitted more by sleep when they stem from difficult tasks (Empson & Clarke, 1970; Tilley & Empson, 1978), when more daytime learning was dedicated to encoding them (Walker & Stickgold, 2004), if they were explicitly (i.e., intentionally) encoded (Diekelmann et al., 2009), and if they were originally weakly encoded (Diekelmann et al., 2009).

Cognitive expectations also impact the degree of consolidation. For example, monetary rewards for skillful performance improved consolidation of a finger-tapping task (Fischer & Born, 2009). Mere expectation of a post-sleep test, described to participants *after* studying the material, increased slow-oscillation activity and spindle count during SWS, and these parameters correlated with increased performance the next day (Wilhelm et al., 2011). In another study, participants were told to remember some items and to forget others. An increase in hippocampal activity was seen at recall for items slated to be remembered but only if participants slept before being tested (Rauchs et al., 2011). These studies suggest that sleep-enhanced consolidation is highly influenced by factors that attend the original memory representation.

The temporal ordering of ripples followed by spindles is suggestive of the transfer of information from the hippocampus to the cortex (Andrade et al., 2011). Sleep in general, but stage 2 in particular, enhances functional connectivity between the hippocampus and the medial prefrontal cortex (mPFC; Gais et al., 2007). Although it was previously thought that information in this pathway was only directed from the hippocampus to the cortex (Hasselmo & McClelland,

1999), a recent study showed that it was bidirectional, which suggests that the cortex actually is prompting retrieval from the hippocampus during sleep (T. Wagner, Axmacher, Lehnertz, Elger, & Fell, 2010).

During other stages of sleep, the hippocampus is connected actively at different times to the primary motor cortex, the anterior cingulate cortex, and the occipital cortex (Andrade et al., 2011), possibly reflecting the consolidation of rapidly-formed, hippocampal-dependent memories to distal sites in the association cortex during sleep. Oddly, as sleep gets deeper, activity in hippocampal connections to the brain's default network becomes less pronounced (Andrade et al., 2011). This is another reason why it remains unclear what specific advantages SWS might provide over the benefit of stage-2 sleep alone.

REM sleep. The majority of REM sleep occurs during the second half of the night (Walker & Stickgold, 2004). As previously mentioned, some research has suggested that SWS benefits the retrieval of declarative memories, and that REM sleep facilitates the consolidation of procedural and emotional memories (Diekelmann et al., 2009), as well as enhancing creative processing of information (Walker et al., 2002).

The mechanism for REM-sleep consolidation appears to be ponto-geniculate-occipital (PGO) waves (or pontine waves in rodents). The neural pathway of PGO waves, which originate in the pons and travel through the thalamus to the occipital cortex, reflects an interaction between the motor and visual systems. The neurons in this pathway frequently fire during waking activity but are potentiated by motor and sensory neurons in the peripheral nervous system. As motor output and sensory input are blocked during REM sleep, PGO waves are spontaneously generated by "executive" neurons in the pons (Hobson & Pace-Schott, 2002). Although PGO waves have not been studied to the same extent as ripple-spindle events, it has been suggested

that PGO waves may reflect neural reactivation of waking motor and sensory activity in much the same way that ripple-spindle events reflect the reactivation of declarative information (Datta, 2006).

The density of PGO waves during REM sleep is highly correlated with the retention of pre-sleep learning (Datta, 2000). Additionally, when pontine waves are experimentally induced in rodents, procedural memory consolidation occurs, even when subjects are deprived of REM sleep (Datta, Mavanji, Ulloor, & Patternson, 2004). The phase-locked combination of PGO waves with cortical theta waves in REM sleep (Holscher, Anwyl, & Rowan, 1997) determines whether long-term potentiation or long-term depression will occur in the hippocampus (Pavlides, Greenstein, Grudman, & Winson, 1988). When PGO waves are experimentally induced at the peak of a theta wave, long-term potentiation occurs (Holscher et al., 1997). Alternatively, when PGO waves are counter-synchronous with theta waves (i.e., they begin at the trough of theta waves), long-term depression occurs. Also, the zif-268 gene is upregulated during REM to facilitate synaptic plasticity, thereby improving the effectiveness of PGO waves in consolidating nondeclarative memories (Ribeiro et al., 2002).

The Influence of Sleep on Pattern Separation and Pattern Completion

In addition to strengthening memories, sleep also appears to increase memory specificity. For instance, using the Deese–Roediger–McDermott (DRM) paradigm, several researchers have demonstrated that sleep decreases the prevalence of false memories (Fenn, Gallo, Margoliash, Roediger, & Nusbaum, 2009; Payne et al., 2009) and that sleep deprivation increases them (Diekelmann, Landolt, Lahl, Born, & Wagner, 2008). This suggests that sleep may help to facilitate the strengthening of the details of memories (rather than the overall gist of memories).

However, there is also evidence that sleep-dependent consolidation actively erases irrelevant memories or memory components (Crick & Mitchinson, 1983; Walker & Stickgold, 2004). For instance, one study found that, although memory for details of a previously-depicted emotional event (e.g., a picture of a car wreck) improves after sleep, memory for the context of that event (e.g., details regarding the setting) is worse following sleep than after an equivalent waking delay (Payne & Kensinger, 2010). Another study presented participants with items designated as "to be remembered" and "to be forgotten." Several days later, participants who were allowed to sleep each night had better memory for the items to be remembered, but participants deprived of a single night of sleep persisted in recognizing the items that were to be forgotten (Rauchs et al., 2011). This suggests that sleep deprivation disturbed the process of intentional forgetting.

Given the evidence cited here, it is difficult to say whether pattern separation or pattern completion would more likely result from sleep. On one hand, some research suggests that sleep strengthens memory for details, making memories more specific. The proposed mechanism for such specificity is the reactivation of hippocampal neural circuits, which may result in pattern separation processes. On the other hand, sleep also appears to facilitate the forgetting of details, which could occur as memories are consolidated to the highly networked but nonspecific neurons of the cortex, and would result in pattern completion. We are not aware of any studies, to date, that have directly investigated the effect of sleep on the behavioral responses of pattern separation and pattern completion following sleep. Experiments 1 and 2 addressed this question.

Chapter 2: Specificity of Memory for Pictures (Experiment 1)

Although pattern separation and pattern completion may be considered neural computations reflecting particular approaches to encoding and retrieval, in behavioral studies, only the *effects* of these processes can be assessed (Santoro, 2013). Pattern separation is needed to discriminate a stimulus from a previously-presented similar stimulus. Pattern completion, on the other hand, is needed in order to retrieve a previously-stored representation given a degraded cue, such as a similar but not exact stimulus. Accordingly, for the purposes of the current study, we inferred pattern separation and pattern completion processes according to participants' ability to recognize stimuli as distinct from or similar to previously-presented stimuli. Attending to differentiating details reflected pattern separation; attending to similarities reflected pattern completion (Duncan et al., 2012; Holdstock et al., 2002).

Participants in Experiment 1 viewed a sequence of images of everyday objects and performed an old/new recognition memory task immediately after encoding and again after a 12-hr delay. For one group of participants, the delay occurred during the day (the Wake condition) and for another group of participants the delay occurred overnight (the Sleep condition). In the recognition memory test, participants were shown either exact repeats (targets) or similar, but not exact stimuli ("lures"), with the degree of similarity parametrically varied. Participants indicated whether each stimulus was "same" or "different" and then gave a confidence rating for their decision. We planned to compare the quadratic trend interaction of the sleep and wake conditions along the dimension of similarity using orthogonal polynomial contrasts. A significant interaction would indicate that different computations were being employed in the wake and sleep condition. As mentioned in the previous chapter, these methods were used in order to determine whether sleep benefits pattern separation or pattern completion.

Method

Participants

Fifty participants (ages 17-28, *M* = 20.3, *SD* = 2.2; 21 males, 22 females, 7 unidentified) were recruited from the student body of Brigham Young University and received course credit in exchange for their participation. All participants gave written informed consent prior to participating in the study.

Materials

A rating process was used to select the images for the current study. Nine-hundred-and-seventy-six pairs of images were obtained using online image searches (see Figure 1 for examples). Only one pair of stimuli was used to represent a specific item (e.g., only one pair of watermelon pictures was used) in order to control for potential overlapping interference across stimuli.

Thirty-five participants, independent from the sample who eventually participated in Experiment 1, rated the similarity of the picture pairs on a 7-point Likert scale (1 = "very similar", 7 = "not similar"). Pairs of stimuli were presented using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) for Matlab (Natick, MA). Images were presented until participants made a selection on the rating scale. Ratings that participants assigned faster than 0.5s were removed from this norming process with the assumption that this was not enough time to evaluate similarity (< 1% of total ratings). Given the removal of these stimuli, and because not all participants finished the rating procedure, some picture pairs were rated by fewer subjects than others (*M* = 31.2, range = 27-35).

The standard deviation of the similarity rating of most pairs was between 1 and 2 points, and the intraclass correlation across raters was *r* = .30, both of which indicate fair between-rater

agreement. The picture pairs were rank-ordered by the size of the standard deviation, and the 76

pairs of items that had the largest standard deviations (i.e., those pairs with the poorest between-

rater agreement) were removed, leaving 900 pairs of pictures for use in the current study. Most

of the picture pairs removed had been rated between 3 and 5 on the 7-point scale, suggesting that

picture pairs may have been hardest to rate when they fell in the middle of the scale. The 900

pictures were rank ordered and divided into five equally-sized similarity bins (1 = most similar, 5

= least similar) based on mean similarity scores.
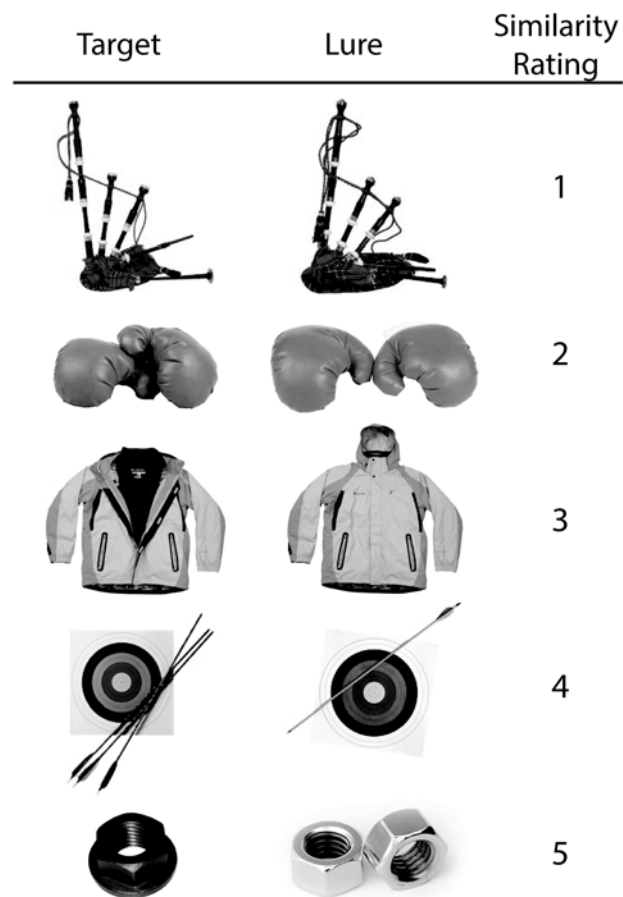
Figure 1. One sample image pair from each of the five similarity ratings bins, arranged from

most similar (1) to least similar (5).

A survey asking participants about their previous night's sleep was adapted from the Pittsburgh Sleep Quality Index (Buysse, Reynolds, Monk, Berman, & Kupfer, 1989). The survey asked participants to report about their previous night's sleep such details as the number of hours slept, the overall quality of sleep, and their level of arousal at the time of the survey (see Table 1 for survey results).

Table 1

Summary Statistics from the Sleep Survey

	Mean	*SD*	Percent
Total sleep last night (in hours)	6.6	1.1	-
Level of tiredness at time of survey	2.1	0.6	-
Self-reported ACT score	27.8	3.6	-
Exercised in the last 24 hours	-	-	24%
Had trouble sleeping last night	-	-	15%
Took medicine to help sleep last night	-	-	4%

Note. At the end of Experiment 1, participants provided this information in a brief survey. The data in the table are for all participants, not separated by group. The level of tiredness was rated on a 4-point scaled where 1 was "not at all" and 4 was "utterly exhausted". *SD* = standard deviation.

Design and Procedure

Experiment 1 consisted of a study phase, an immediate recognition memory test, and another recognition test following a 12-hr delay. During the study phase, one image at a time (the order was randomly selected for each participant) from each of the 900 picture pairs was

presented to participants for 2500 ms using E-Prime 2.0 (Schneider, Eschman, & Zuccolotto, 2002). To ensure that participants attended to the images, participants were instructed to memorize the picture details for a later test and were asked to press one of two keys, indicating whether the item ordinarily would fit inside a shoebox or not. Immediately following the study phase, participants performed the first recognition test. During this test phase, 75 of the pictures were identical to the target pictures previously studied; the other 375 "lures" were different from the target in varying degrees of similarity (75 from each of the five similarity bins). Participants indicated by button press whether each picture was the "same as" or "different from" the one they saw in the study phase. Participants then rated the confidence of their response on a 3-point scale (1 = very confident, 3 = not at all confident). Both same/different judgments and confidence ratings were self-paced.

After the first session was completed, participants left the laboratory and were asked to return again 12 hrs later to complete the second test. The second test was identical in procedure to the first and used the remaining 450 target-lure pairs. Upon completion of the second test session, participants completed the modified Pittsburg Sleep Quality Index.

This procedure deviated from previous studies of pattern separation for images (Bakker et al., 2008; Duncan et al., 2012; Kirwan et al., 2012; Kirwan & Stark, 2007) in several important ways. First, because encoding and retrieval were separated by 12 hrs, it was impractical to utilize a continuous recognition procedure, wherein the lure and repeated images are interweaved within a series of new pictures. Second, there was an imbalance between the number of repeats and lures. This was necessary in order to accumulate a sufficient number of responses in each similarity bin to assess a performance trend across the variable of similarity. Also, because of the large number of lure trials needed to assess performance at each level of similarity, there

were no completely novel images in the test phase in order to reduce the number of test-phase trials. Although these changes precluded us from directly comparing the current findings to those of previous studies, the current task allowed for more precision in analyzing responses to the lure stimuli.

Importantly, the 12-hr delay occurred either during the day (e.g., 9 a.m. to 9 p.m.) or during the night (e.g., 9 p.m. to 9 a.m.) and was determined by the appointment time for which each individual registered to participate. Participants in the sleep condition ($n = 29$) were asked to sleep according to their typical schedule and those in the wake condition ($n = 21$) to go about their normal daily activities. Although this design did not control strictly for time-of-day effects, it is the most common design used in the sleep literature. Moreover, the literature makes clear that it is sleep *per se*, and not the timing of the delay, that promotes memory consolidation (Fischer et al., 2002; Koulack, 1997).

Results

Overall recognition-memory performance was good for both sleep and wake groups in the immediate and the delay tests. Table 2 lists the hit/miss rate ("same" and "different" responses to repeated stimuli, respectively) and the false alarm/correct rejection rate ("same" and "different" responses to lure stimuli, respectively) for the sleep and wake groups in the immediate and delayed tests. For the miss rate, a 2 (immediate, delay) × 2 (sleep, wake) ANOVA revealed a main effect of delay, $F(1,48) = 40.94$, $p < .001$, but no main effect of sleep condition and no sleep × delay interaction. There were no main effects or interactions for the correct rejection rates. We also calculated a discriminability score (d') for each condition with lure stimuli collapsed across similarity. A 2 (immediate, delay) × 2 (sleep, wake) ANOVA revealed a main effect of delay on d', $F(1,48) = 50.80$, $p < .001$. Planned comparisons revealed a

significant difference in discriminability scores after a 12-hr delay for the sleep and wake groups, $t(48) = 2.33$, $p < .05$, two-tailed test. These results are consistent with a benefit of sleep on overall memory performance after a 12-hr delay.

Table 2

Discriminability of Target Pictures and their Corresponding Lures

Condition	Hit Rate / Miss Rate	False Alarm Rate / Correct Rejection Rate	d' (*SD*)
Immediate			
Sleep	.62 / .38	.26 / .74	.99 (.36)
Wake	.62 / .38	.28 / .72	.92 (.30)
Delayed			
Sleep	.53 / .47	.26 / .74	.79 (.30)*
Wake	.51 / .49	.29 / .71	.60 (.25)*

Note. Hit rate and false alarm rate are presented for all pictures with similarity collapsed. Discriminability (d') and its standard deviation (*SD*) are also presented for the sleep and wake conditions at both the immediate and delayed tests. The discriminability of memory scores was significantly higher in the delayed sleep than the delayed wake group, indicating better memory performance. * $p < .05$.

We next examined the effects of target-lure similarity on memory performance. We anticipated that, in general, the percent of "different" responses would gradually increase as the lure stimuli became more dissimilar from their respective targets. Of critical importance, we predicted that any differences in the curvilinearity of the responses to different similarity levels following the waking delay versus the sleep-filled delay would reflect differences in underlying

neural computational processes. If performance followed a linear trend, it would suggest that no additional neural computations were occurring, but concave and convex curvilinear trends would suggest increased biases toward pattern separation and pattern completion, respectively (Yassa & Stark, 2011). In other words, if the brain performed neither pattern separation nor pattern completion, a linear increase in similarity should merit a linear increase in correct rejections. However, if participants engaged in pattern separation, we should see a sharp increase in correct rejections even after a small change in target-lure similarity. And, if participants engaged in pattern completion, we should see that large changes in target-lure similarity were required before the percent of correct rejections increased.

In order to investigate these performance trends, the proportions of "different" responses to lures were subjected to a mixed ANOVA, using delay type (immediate, delayed), degree of similarity (five levels), and response confidence (high, medium, low) as fixed, within-subject factors, and sleep condition (sleep, wake) as a fixed, between-subjects factor (Figure 2). In a preliminary analysis, we also included the covariates listed in Table 2. Because none of these variables was a significant predictor of memory performance, and because their inclusion did not alter the main effects or interactions, we report the simpler analysis without them. There was a significant main effect of similarity, $F(4,148) = 14.01$, $p < .001$, as well as a significant confidence × similarity interaction, $F(8,264) = 5.61$, $p < .001$. The three-way interactions of delay × confidence × sleep condition, $F(8,66) = 3.72$, $p < .05$, and delay × confidence × similarity, $F(8,264) = 2.24$, $p < 0.05$, were also significant. The four-way interaction of delay × confidence × similarity × sleep condition was not significant, $F(8,264) = 0.67$, $p = .72$.

Our critical planned comparison was between the quadratic components of the "different" responses to lures in the delayed-test condition for the wake vs. sleep groups. For responses made with high confidence, there was a significant quadratic sleep condition × similarity
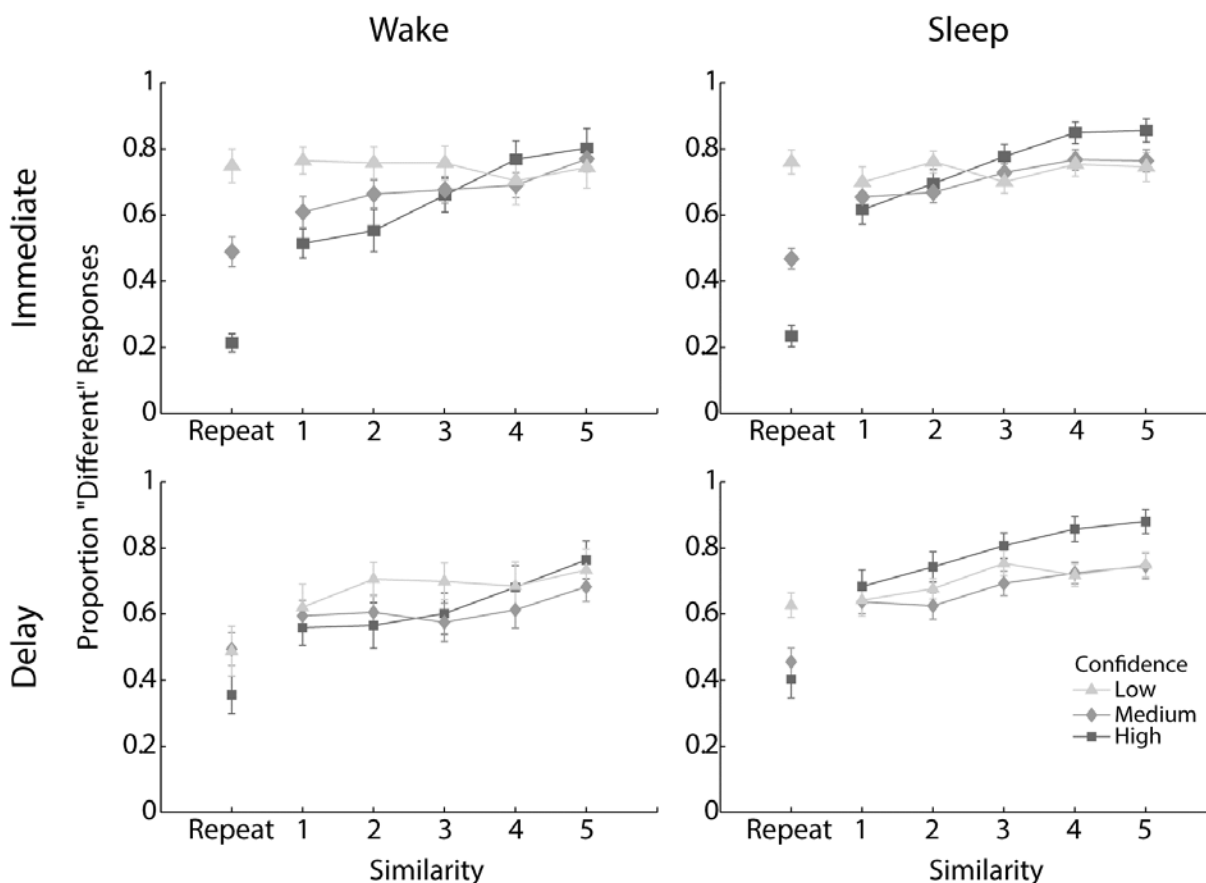
Figure 2. The proportion of "different" responses by level of similarity in Experiment 1. Participants were given a recognition memory test with repeated stimuli (repeat) or related lures that varied in similarity from high (1) to low (5). Participants responded "same" or "different" and gave a confidence rating ("low", "medium" or "high") for each stimulus. Participants were tested both immediately following the study phase (top row) and following a 12-hr delay (bottom row). The Wake group (left column) had a waking delay while the Sleep group (right column) slept during the delay period. Error bars depict SEM.

interaction, $F(1,46) = 6.99$, $p < .05$ (Figure 3). The quadratic components of the sleep group ×

similarity interactions for responses made with medium and low confidence failed to reach

significance ($ps > .15$). Furthermore, a similar analysis of the quadratic sleep condition ×

similarity interaction of high confidence responses in the immediate condition was not

significant, $F(1,47) = 1.93$, $p = .17$. This suggests that, for decisions made with high confidence,

curvilinear performance trends of subjects in the two sleep conditions differed from each other

after the 12-hr delay but not before.
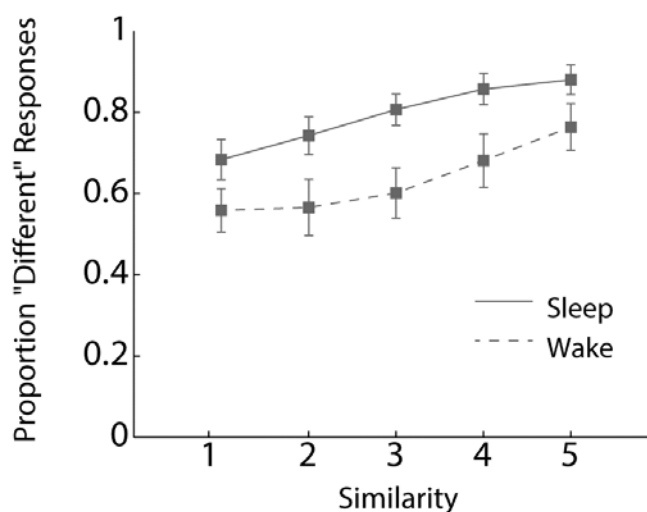
Figure 3. The proportion of "different" responses by similarity for the high-confidence responses

in the delay condition. There was a significant sleep group by similarity quadratic interaction,

indicating different similarity response functions following a sleep- or wake-filled delay. Error

bars depict SEM.

Discussion

We found that the pattern of responding was different across the sleep and wake

conditions. Specifically, participants were more likely to generalize across similar stimuli

following a waking delay, even when recognition-memory decisions are made with high

confidence. This suggests a greater bias toward pattern completion processes following a waking delay and a greater bias toward pattern separation processes following a delay that includes sleep. These findings lend support to other studies that have shown that one night of sleep benefits memory for details (van der Helm, Gujar, Nishida, & Walker, 2011). This benefit is evident in the higher proportion of "different" responses to similar lures in the sleep group relative to the wake group. Because memory for detail is hippocampal-dependent, such findings suggest that memories are being retained in the hippocampus after a single night of sleep.

The CLS model predicts a process of systems consolidation, wherein memory representations are gradually transferred from the hippocampus to the cortex. By storing a representation in the cortex, the brain is figuratively filing the memory in a network of other, related memories (Alvarez & Squire, 1994), resulting in more generalized, stable, and useful— but less specific—memories than existed prior to sleep. Although it seems obvious that memory representations would not be transferred entirely to the cortex in a single night (a supposition supported by the present study), it remains unclear how long the process of consolidation requires. For instance, previous research has shown that one night of sleep provides creative solutions to cognitive puzzles (U. Wagner, Gais, Haider, Verleger, & Born, 2004) and benefits consolidation of related word pairs (Gais & Born, 2004) but not unrelated word pairs (Meienberg, 1977). Such findings suggest that, even with a single night's sleep, people can access some of the benefits of cortically-dependent memories.

However, we found evidence of pattern separation processes after one night of sleep, a computation that would be much less likely to occur after systems consolidation. The respective roles of the hippocampus and cortex in the first few days after encoding a memory, therefore, remain unclear. Some types of tasks might be benefitted by retrieving information from the

cortex (e.g., conceptual, relational, or applied tasks), while other types may capitalize on retrieval from the hippocampus (e.g., those that require memory for specific details, like the task used in the current experiment). It is possible that during the first few days after encoding, people are able to utilize either of two representations, depending on task demands. This account may also help explain why consolidation fulfills multiple functions (e.g., both stabilization and enhancement; see Walker & Stickgold, 2004).

Because we believe conceptual or applied types of tasks are more likely to benefit from pattern completion, the following experiment applied similar methods as used in Experiment 1 to semantic stimuli. This allowed us to test whether sleep affects the quality of memory in a ubiquitous fashion, or whether, conversely, the impact of sleep on memory is moderated by the type of material being learned or by contextual demands on memory.

Chapter 3: Specificity of Memory for Discourse (Experiment 2)

Experiment 1 assessed the effects of sleep-dependent consolidation on pattern separation and pattern completion processes for single objects. These results extend a number of previous studies that have examined pattern separation and pattern completion using single objects (e.g., (Bakker et al., 2008; Duncan et al., 2012; Kirwan et al., 2012; Kirwan & Stark, 2007). Experiment 2 sought to extend these findings to a more applied task with two goals: first, to determine if the pattern of results obtained for single objects extended to more semantically-laden domains, and second, to better characterize the practical applications of memory specificity and generalization due to the influence of sleep-dependent consolidation on pattern separation and pattern completion processes.

Memories of a specific, detailed nature are necessary for some tasks but less useful for others. In order to perform well on an exam, for instance, students often must recall precise details from course lectures and readings. After the exam, it is more beneficial for students to consolidate the gist of the material into networks of related information. However, it is unlikely that the brain has a toggle mechanism in place to mediate the differential consolidation of memory before and after an exam. For this reason, it is difficult to predict what role sleep might play in the consolidation of semantic information.

To answer this question, participants read a selection from an introductory psychology textbook and answered a series of true/false questions. Although the stimuli diverged from those in Experiment 1, the design of Experiment 2 remained much the same. The most notable difference was the elimination of the immediate test condition from Experiment 2. As in Experiment 1, most of the test items were false, with the degree of falsity parametrically varied so that some items were more similar to the material presented in the textbook.

Method

Participants

Thirty participants (ages 18-28, $M = 21.9$, $SD = 2.4$; 14 males, 16 females) were recruited from a single section of an introductory psychology course, gave written consent, and were provided extra credit for their participation. Although this is a small sample for a study investigating sleep-dependent consolidation, there were only 32 students enrolled in the class. Additional students could not be recruited using an alternative medium without sacrificing the external validity of the design.

Materials

We developed a true/false test based on the content of a single chapter of an introductory psychology textbook (Rathus, 2001). As in Experiment 1, we sought a large lure-to-target ratio. We originally wrote 90 false statements and selected 90 quotations from the text that refuted them. We asked 12 trained raters to judge the similarity between the false items and textbook quotations on a 3-point Likert scale ranging from "not similar" (1) to "very similar" (3). These ratings were ordered by the size of the standard deviation for each false statement, and the 10 items that had the largest standard deviations (i.e., those with the lowest between-rater reliability) were removed, leaving 80 false items for the test. These mean similarity ratings were used to group the items into five levels of falsity (16 items in each bin). We then wrote 20 true items for a total test length of 100 true/false items.

Design and Procedure

Students who volunteered to participate were randomly assigned to read a chapter from an introductory psychology textbook during either the morning or the evening ($n = 15$ in each condition). Students were invited to choose any day to read the chapter within a one-week span

of time. The chapter was made available electronically for up to 2 hrs. Twelve hours after reading the chapter, students completed the true/false test and the modified Pittsburg Sleep Quality Index (see Table 3 for survey results) online via (Qualtrics Labs, 2012). The 12-hr delay was verified by comparing the electronic timestamps recorded when the textbook chapter was opened against the time when the test was initiated.

Table 3

Summary Statistics from the Sleep Survey

	Mean	*SD*	Percent
Total sleep last night (in hrs)	6.4	1.2	-
Level of tiredness at time of survey	2.3	0.6	-
Self-reported ACT score	26.8	2.7	-
Exercised in the last 24 hrs	-	-	27%
Had trouble sleeping last night	-	-	17%
Took medicine to help sleep last night	-	-	3%

Note. At the end of Experiment 2, participants provided this information in a brief survey. The data in the table are for all participants, not separated by group. The level of tiredness was rated on a 4-point scaled where 1 was "not at all" and 4 was "utterly exhausted". *SD* = standard deviation.

Results

Overall memory performance was good following the 12-hr delay, with performance slightly better following sleep, consistent with a role of sleep in consolidation. Hit/miss rates and correct rejection/false alarm rates for the sleep and wake groups are presented in Table 4.

As in Experiment 1, the miss rate was smaller following sleep than following a waking delay, $t(28) = 2.69$, $p < .05$. Similarly, a two-tailed t-test showed that discriminability was better following a delay containing sleep (mean d' = 1.25, $SD = .54$) than a waking delay (mean d' = .85, $SD = .62$) with marginal significance, $t(28) = 1.90$, $p = .07$.

Table 4

Discriminability of False Items and Corresponding True Quotations

Condition	Hit Rate / Miss Rate	False Alarm Rate / Correct Rejection Rate	d' (*SD*)
Sleep	.84 / .16	.44 / .56	1.25 (.54)
Wake	.76 / .24	.45 / .55	.85 (.62)

Note. Hit rate and false alarm rate are presented for all items with falsity collapsed. Discriminability (d') and its standard deviation (*SD*) are also presented for both conditions. The difference in discriminability across conditions was marginally significant, $p = .07$.

Similar to Experiment 1, we anticipated that the percent of "false" responses would gradually increase as the items' degree of falsity increased. The percent of "false" responses to false items was subjected to a mixed ANOVA with degree of falsity (five levels) as a fixed, within-subject factor, and sleep condition (sleep vs. wake) as a fixed, between-subjects factor. There was a main effect of falsity $F(4,112) = 64.83$, $p < .001$. However, in contrast to Experiment 1, a test of within-subjects contrasts revealed a significant linear trend interaction between falsity and sleep condition, $F(1,28) = 4.70$, $p < .05$ (Figure 4), but not a quadratic trend interaction, $F(1,28) = 0.03$, $p = .871$, suggesting that the linear pattern of performance differed depending on whether students slept or stayed awake.
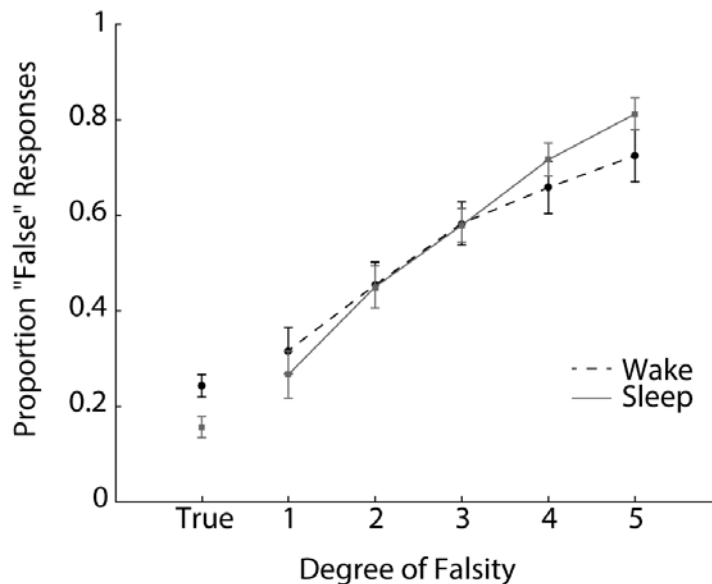
Figure 4. The proportion of "false" responses by degree of falsity in Experiment 2. Participants were given a true/false test after reading a textbook chapter. The false items varied in their degree of falsity from low (1) to high (5). The Wake group had a waking delay while the Sleep group slept during the delay period. Error bars depict SEM.

Discussion

The results of Experiment 2 suggest that the pattern of retrieval for academic material depends on whether students sleep before being tested. The significant linear interaction between the two sleep conditions, consistent with a visual inspection of Figure 4, suggests that following sleep there is better discrimination for more obviously false items but also increased generalization for false items that were more similar to the text. Because both performance trends are linear, we did not find evidence for a bias toward either pattern separation or pattern completion in the retrieval of information encoded from the textbook chapter, regardless of their sleep condition.

There are several possible reasons why the trend lines may be straight in both conditions of Experiment 2, despite our having observed quadratic functions in Experiment 1. First, because of the increased external validity of Experiment 2, we were unable to maintain the same level of control over how well participants encoded the original stimuli. In Experiment 1, participants made an immediate behavioral response to every image shown (i.e., they indicated whether it would fit in a shoebox) and the exposure time to each stimulus was controlled (2s). In Experiment 2, we verified that students accessed the textbook chapter for the specified time, but we were unable to control the depth of processing or exposure time to each subsequently-tested statement. Furthermore, the information in the textbook was more abstract than the images of Experiment 1. Accordingly, it is possible that students did not encode the information as thoroughly or concretely in Experiment 2. A second possible explanation depends on a minor methodological difference between the experiments. In Experiment 2, there were fewer test stimuli (only 80 false items) than in Experiment 1 (375 "lure" images). There were also fewer participants, and we did not ask participants to rate their level of confidence for each response in Experiment 2. It is, therefore, possible that our behavioral measure was not sufficiently sensitive to detect small differences in computational biases.

Finally, it is possible that there is an actual difference between the computational processes involved in memory for semantic information and image processing. Additional studies investigating pattern separation and pattern completion in applied settings are needed before we can confidently conclude whether automated computations are involved in these types of memory.

In order to discover whether sleep predisposes individuals toward pattern separation or pattern completion, in Experiments 1 and 2, we tested recognition memory for two different sets

of stimuli. In both studies, the similarity between studied targets and tested lures was parametrically varied. Our results demonstrate that sleep-dependent consolidation produced better recognition-memory discrimination for simple objects, consistent with increased pattern separation processes. When stimuli are more complex, however, as when we tested recognition memory for semantic information, there was no evidence for an increased bias toward either pattern separation or pattern completion regardless of whether participants slept during the 12-hr delay.

Importantly, we utilized a novel behavioral approach to studying recognition memory performance in these two experiments. This approach may prove useful in allowing researchers to investigate computational processes in more realistic situations as it becomes validated against established neuroimaging methods. Future work in this area should endeavor to reconcile the conflict between what appear to be robust, short-term benefits of sleep on memory accuracy with longer-term decreases in memory specificity that are also thought to depend on sleep.

Chapter 4: Consolidation of Early- and Late-Encoded Memories (Experiment 3)

Students who take college classes earlier in the morning generally get better grades than those whose classes begin later in the day (Onyper, Thacher, Gilbert, & Gradess, 2012). Ironically, however, few students learn well in early classes or perform well on tests administered in the morning (Dunn, 1998). Sleep research has also generally found that information is best learned at night. For instance, Gais, Lucas, and Born (2006) showed that information studied directly before sleeping is better consolidated than information learned earlier in the day. Their participants studied a list of vocabulary words in either the morning or the evening and their memory was tested either 24 or 36 hrs later. Participants who studied in the evening performed better on the memory task than those who studied in the morning. A follow-up experiment demonstrated that this could not have been due to time-of-day effects. Importantly, the length of the retention interval did not have any effect on memory, suggesting that the benefit to memory from sleeping shortly after encoding is derived from the timing of sleep and *not* from having a shorter retention period prior to testing.

However the prior study did not control for daytime forgetting, so it remains unclear whether sleep preferentially benefits the consolidation of information learned in the evening over information learned in the morning or whether the discrepancy in consolidation of morning and evening learning is due to daytime forgetting. In other words, it is possible that, when accounting for the amount of forgetting that occurs during wakefulness, sleep may equally benefit the consolidation of all the representations formed throughout the day, but that it strengthens the representations as they exist at the time of sleep onset, not as they existed when they were first encoded. Alternatively, it is possible that sleep disproportionately benefits

information learned in the evening, consolidating recently encoded information to a greater extent than what remains of a memory that was originally encoded in the morning.

As mentioned in Chapter 1, sleep is thought to protect memories from the decay and interference of waking activities. In the process of creating a wake and sleep group, Experiments 1 and 2 (together with many previous sleep studies) confound wake with the process of decay, because wake groups are necessarily exposed to more decay than sleep groups. By measuring and accounting for the amount of daytime forgetting that occurs prior to sleep onset, Experiment 3 attempted to demonstrate how the time of day at learning affects sleep-dependent consolidation. Experiment 3 was further designed to illustrate the degree to which the findings of previous sleep studies are actually due to sleep as opposed to the significant decrease in decay that is often conflated with groups of experimentally-designated sleeping participants.

Method

Participants

We recruited 378 participants from the student body of Brigham Young University. Forty-five participants were excluded from the analysis because they did not take the follow-up test at the specified time, leaving 333 participants in the present study (ages 16-59, $M = 20.9$, $SD = 4.9$; 45% males, 55% females). All participants gave written informed consent prior to participating in the study and received course credit in exchange for their participation.

Design and Procedure

This final experiment differed radically from Experiments 1 and 2 in both methods and theoretical intent. In order to demonstrate the subtle gradations in the overall pattern of recognition memory performance, the previous studies employed a recognition task for pictures

and statements. In contrast, Experiment 3 utilized a recollection task for word pairs because the intent was to evaluate overall memory scores.

Specifically, Experiment 3 was designed to determine whether the oft-cited benefit of sleep to declarative memory occurs equally for memories formed in the morning or in the evening if decay in the memory representation prior to sleep onset is controlled. Therefore, in Experiment 3, each participant viewed 120 English nouns (3-11 letters in length). Words were paired semantically (e.g., copper-penny) so that each participant viewed 60 word pairs. We used semantically-related pairs for comparability with previous research (e.g., Plihal & Born, 1997) and because unrelated word pairs are not consolidated during sleep (Meienberg, 1977). The word pairs in this study were matched for word length (both words contained the same number of syllables and differed by no more than one letter in length), and the list had a mix of high- and low-frequency words, but the words in each pair fell within the same use-frequency range (within 20 words per million of each other for the general population). All words had free-association strengths between 0.08 and 0.25, and normalized concreteness ratings were greater than 400. The word pairs were originally constructed by Voss and Federmeier (2011).

Each pair of words was presented side-by-side in the center of a computer monitor using E-Prime 2.0 (Schneider et al., 2002). Pairs were presented for 4000 milliseconds, and a central fixation cross was presented during a 1000 millisecond interstimulus interval. Participants were asked to memorize the word pairs in whatever way worked best for them because they later would take a memory test online at home in which the first word of each pair would be presented as a cue, and they would be asked to provide the second word. Again, we chose a cued-recall task instead of a recognition memory task for comparability with previous research, but also

because sleep benefits recollection memory tasks more reliably than recognition tasks (Drosopoulos, Wagner, & Born, 2005).

After participants had studied the word list, they were given a URL to complete the test online at a designated time via Qualtrics Labs, Inc. (2012) software. The test simultaneously presented the 60 cue words in an order randomized across participants. They then completed the modified Pittsburgh Sleep Quality Index (see Table 5 for summary statistics).

Table 5

Summary Statistics from the Sleep Survey

	Mean	*SD*	Percent
Total sleep last night (in hrs)	7.0	1.4	-
Level of tiredness at time of survey	2.4	0.7	-
Self-reported ACT score	27.9	3.6	-
Exercised in the last 24 hrs	-	-	26%
Had trouble sleeping last night	-	-	19%
Took medicine to help sleep last night	-	-	5%

Note. At the end of Experiment 3, participants provided this information in a brief survey. The data in the table are for all participants, not separated by group. The level of tiredness was rated on a 4-point scaled where 1 was "not at all" and 4 was "utterly exhausted". *SD* = standard deviation.

Figure 5 illustrates the experimental design. Half of participants ($n = 165$) were randomly assigned to complete the recall test immediately upon waking the next morning (the after-sleep group). The other half of participants ($n = 168$) performed the test immediately

before going to bed (the before-sleep group). In addition, the length of the waking delay differed

across participants. Specifically, the length of time between studying the word pairs and either

taking the test or going to sleep was long for some ($M = 15.78$ hrs, $SD = 1.2$) and short ($M = 4.52$

hrs, $SD = 1.4$) for others, as determined by the appointment time for which each person

registered to participate and the participant's sleep-onset time. A large number of participants in

the long-delay group napped during the course of the experiment ($n = 51$) and a comparable

proportion of participants in the short-delay group had likewise napped earlier in the day ($n = 45$). Accordingly, in order to control for this potential confound, we included napping as an

additional factor in our model.
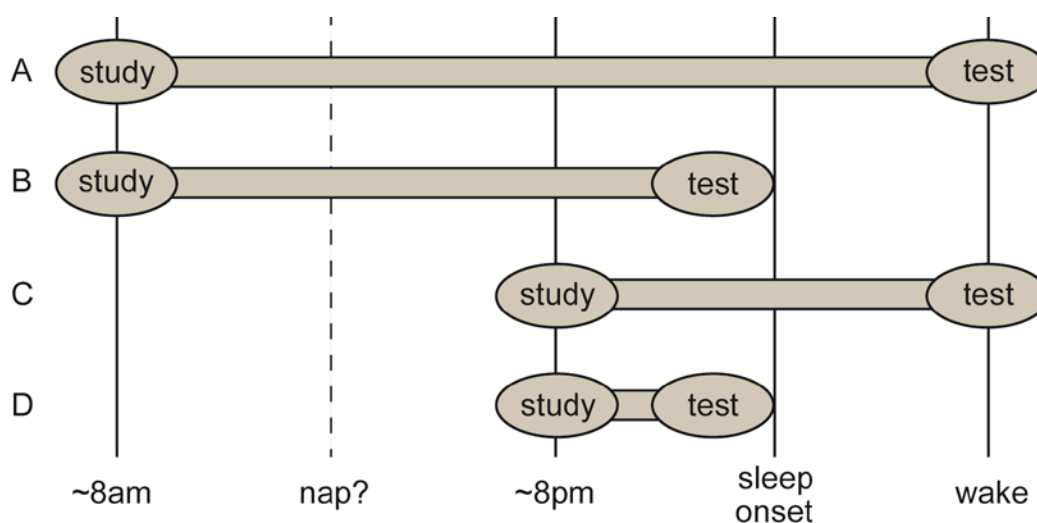
Figure 5. A schematic of the experimental design. Condition A had a long delay and a test after

sleep. Condition B had a long delay and a test before sleep. Condition C had a short delay and a

test after sleep. Condition D had a short delay and a test before sleep. Some participants

voluntarily napped during the experiment (A and B) or earlier in the day before the experiment

began (C and D).

The independent variables were the length of the waking delay (long vs. short delay), whether participants took the test before or after sleeping, and whether participants had napped in the last 24 hrs. The dependent variable was the percent of words correctly recalled during the memory task. Misspelled words were counted as correct as long as they did not spell another word that could have been reasonably paired with the cue word. For instance, if a participant were cued with the word "ascent" and the correct response was "descent," then "decent" and "desent" would have been counted as correct, whereas "descend" would not. Responses given in plural form were also not accepted.

Results

Participants recalled 64% of the words on average ($SD = 18\%$). This average is comparable to the recall of word pairs in previous sleep studies (e.g., 62% in Gais et al., 2006). We anticipated that memory performance would be better in the after-sleep group than in the before-sleep group, but that the difference in the *pattern* of improvement between the long and short delays would indicate how sleep consolidation interacts with the time-of-day at learning. Specifically, a main effect of sleep, absent an interaction with delay length, would suggest that consolidation benefits all memories to the same degree regardless of the delay prior to sleep onset. Alternatively, a sleep × delay interaction would indicate that sleep preferentially benefits the consolidation of some memories over others, depending on the time of day at encoding.

To test this hypothesis, we subjected memory performance to a 2-way ANOVA with sleep and delay as fixed independent factors. There was a significant main effect of delay, $F(1,329) = 25.4$, $p < .001$, but not of sleep ($p > .80$). The sleep × delay interaction was not significant ($p > .90$). However, as previously indicated, this model failed to account for the significant number of participants who took a nap. Accordingly, we also performed a 3-way

ANOVA using delay, sleep, and napping (see Figure 6). In this case, there was a significant main effect of delay, $F(1,325) = 28.3$, $p < .001$, but not of sleep or napping (both ps $> .20$). There was a significant sleep $\times$ napping interaction, $F(1,325) = 3.7$, $p = .05$ (see Figure 7, panel A), and a delay $\times$ napping interaction, $F(1,325) = 4.4$, $p = .04$ (see Figure 7, panel B), but the three-way interaction of delay $\times$ sleep $\times$ napping was not significant ($p > .10$).
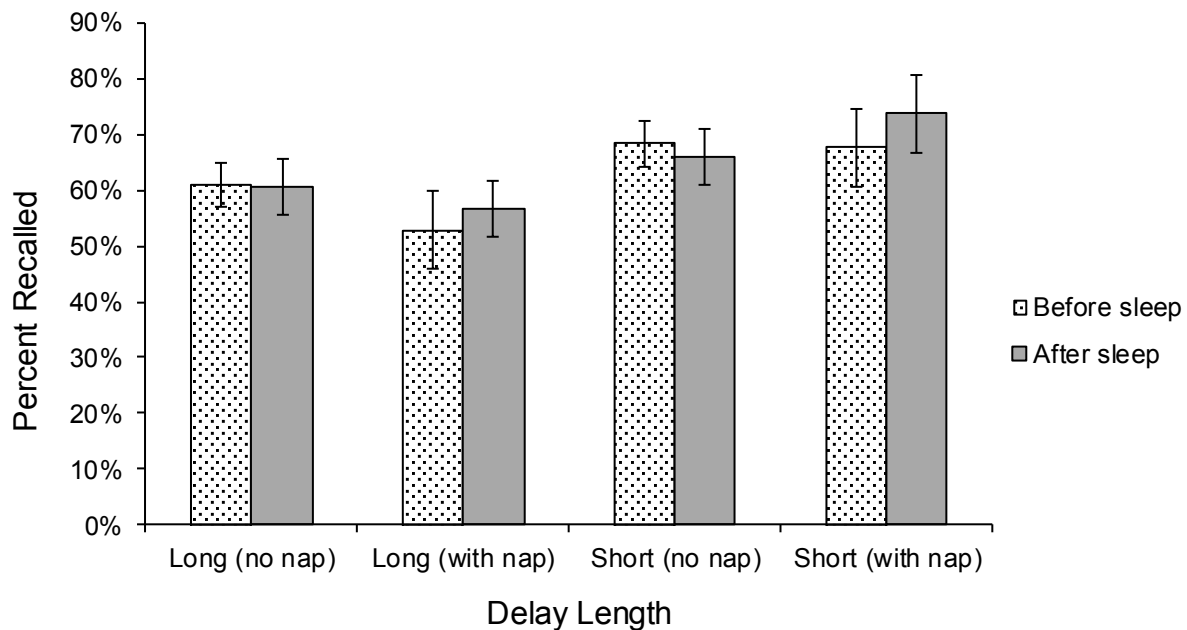
Figure 6. Mean total recall scores for each condition, separated by before/after sleep. Error bars represent the standard error of the mean. There were no significant differences between any of these conditions.

In a second model, we included ACT scores as a covariate (i.e., a proxy for baseline intelligence). ACT scores were a significant predictor of memory performance, $F(1,290) = 28.3$, $p < .001$, and delay remained a significant main effect, $F(1,290) = 43.7$, $p < .001$, but no other main effects or interactions were significant. A two-tailed t-test found that there was no

difference in ACT scores between those who regularly napped and those who did not or between those who had napped in the last 24 hours and those who did not (both $ps > .05$).

Discussion

Interestingly, napping played a much larger role in the performance of our participants than we anticipated. However, because the effects were not robust when ACT scores were included in the model, and because we did not have any *a priori* hypotheses about napping, we offer a guarded interpretation of these results.

The significant sleep × napping interaction collapses the data across the length of delay. Because memory performance was higher in the after-sleep group than in the before-sleep group—but only for those who took a nap earlier in the day—this may suggest that napping somehow provides a mechanism for evening sleep to better promote consolidation (see Figure 7, Panel A). It is difficult to imagine what such a mechanism might entail because previous research suggests no significant differences in sleep architecture between people who nap and people who do not, regardless of age or length of nap (Pilcher, Michalowski, & Carrigan, 2001).

The significant delay × napping interaction (collapsing across the before and after sleep conditions) shows that participants who napped performed more poorly in the long-delay condition than those who did not nap but better in the short-delay condition (see Figure 7, Panel B). Taken together, these two interactions seem to suggest that napping may actually harm the long-term retention of information learned before napping, but may help prepare people to remember information they will learn *later* in the day. In support of this conclusion, one study of older adults found that napping improved accuracy and reaction time on various cognitive tasks they performed later in the day (Campbell, Murphy, & Stauble, 2005). Although no

memory tasks were administered in that study, the results suggested that napping may improve general cognitive fluency or aptitude after napping.
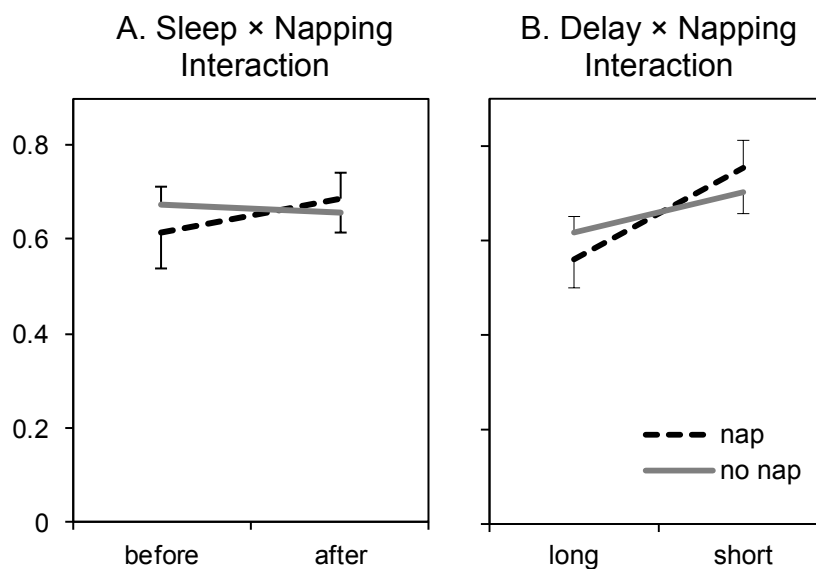
Figure 7. Mean recall scores. Panel A: Sleep × napping interaction (collapsed across delay length). Panel B: Delay × napping interaction (collapsed across before/after sleep). Error bars represent the standard error of the mean.

Still, when ACT was included in the model, these interactions were no longer significant. This, coupled with the lack of significant differences across any two conditions, suggests the interactions may have been artifacts. We have little confidence in our ability to find similar results in future studies of sleeping and napping. Indeed, discrepancies between this study and previous research cast yet further doubt on our findings. For example, it has been shown that memory for word pairs is improved by sleep (Gais & Born, 2004; Plihal & Born, 1997), but we did not find a main effect of sleep in the current study. Rather, in our study, only those participants who voluntarily took a nap appeared to consolidate the word pairs during evening sleep. This may be due, in part, to methodological differences in that previous research required

participants to learn the word pairs to a criterion of 60%, whereas we exposed participants to each word pair only once, which may have added to the variance in the data. In addition, previous research compared post-delay performance against performance immediately after encoding. Using such an approach in the present study would have helped control for pre-existing differences by removing noise due to time-of-day at encoding.

Previous research has further suggested that a nap improves retention of material learned earlier in the day (Tucker et al., 2006), but our findings suggest the opposite. The performance before sleep in participants with a long delay was poorer for those who napped than those who did not, although the participants in our study were not randomly assigned to take naps. It is possible that, on some unknown concomitant measure, the type of person who voluntarily takes a nap is different from the type who does not. However, the lack of difference in ACT scores between these groups suggests that those who voluntarily nap are not more intelligent than those who do not.

The research question this study originally posed remains an important issue to be addressed. A future undertaking of similar research should exert additional experimental control over extraneous variables. For instance, although napping presented itself as an interesting variable for future investigation, preliminary studies should require that participants do not nap. This was not required of participants in the present study because we did not want participants to know that the study's aims involved sleep. This could have introduced an observer effect with the potential of altering normal sleep behaviors. A future study would also benefit from having participants study word pairs to an established criterion, which would increase sensitivity to true effects. This type of pretest would further allow for the calculation of a difference score before and after a delay, thus further reducing inter-subject variance.

Despite the severe limitations inherent in this study, some tentative practical applications may still be observed. For instance, students may need to prioritize their learning. Perhaps one should not take a nap after a particularly difficult class in the morning, but if a student's most difficult class is in the afternoon or evening, it may be beneficial to take a nap before it.

Given the strong and unexpected influence of napping in the present study, future research should give more attention to the interaction of daytime napping and evening sleep. Previous research has largely studied the influence of napping and sleeping as if the two were interchangeable, but the findings of the present study suggest that the story may be more complex.

Chapter 5: Conclusions

Experiments 1 and 2 demonstrated that sleep benefits memory specificity in the short-term. Initially, we hypothesized that the opposite would occur, but our findings indicated that, even if the process of consolidation begins during the first night of sleep, people still have access to the original hippocampal representation. Indeed, participants can probably access the memory either in the cortex or in the hippocampus depending on the task's demands.

The research question posed in Experiment 3 remains largely unaddressed. The protocol should be significantly revised to limit variability across participants before it is used again. The findings also highlighted the importance of daytime napping, which has been treated in the literature as essentially synonymous with evening sleep. In the past, most studies have either compared a daytime nap to a waking delay *or* an evening of sleep to a waking delay. In order to better understand how each type of sleep impacts memory, however, future studies should explicitly compare the two types of sleep to each other.

These experiments confirm the findings of previous studies in which sleep strengthened memories for specific details through the process of hippocampal replay. However, as these memories are transferred to the cortex, they should become less specific. It is counterintuitive for one mechanism (i.e., sleep) to accomplish two strictly opposite functions, but current theories predict that is exactly what it does.

Future research should investigate the process of sleep consolidation over the long-term in a longitudinal study. In order to more fully understand the two-fold process of consolidation, researchers need to identify how long the hippocampus continues to strengthen memories before they become less specific. The difficulty of this task lies in dissociating systems consolidation from mere forgetting, because both processes result in less-specific memories. Furthermore, it is

impossible to dissociate sleep from the passage of time because study participants obviously cannot be deprived of sleep for months at a time. Still, it is possible that a successful study could be designed to enhance consolidation in one group of participants and not in another. Likewise, rates of forgetting could be experimentally manipulated in two additional groups so that, over an extended period of time, the differential shape of memory curves might be an adequate basis for dissociating the effects of consolidation and forgetting.

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