THE SELECTIVE CONSOLIDATION OF DECLARATIVE MEMORIES

by

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LIST OF ABBREVIATIONS

Abbreviation	**Description**
ERP	Event-related Potential
ROI	Region of Interest
LFE	Late Frontal Effect
LPC	Late Positive Component
EEG	Electroencephalography
KSL	Karolinska Sleep Log
PSQI	Pittsburgh Sleep Quality Index
fMRI	Functional Magnetic Resonance Imaging
SWS	Slow-wave Sleep
REM	Rapid Eye Movement
ANOVA	Analysis of Variance

ABSTRACT

During sleep, recently learned memories are stabilized through a process known as consolidation. This process does not uniformly preserve all recent experiences; some memories fade, whereas others become resistant to disruption and appear to last indefinitely. One possibility consistent with recent results is that memory processing during sleep may reflect an adaptive mechanism for evaluating recent experiences and relating them to future goals. The present study was designed to further test this possibility, by determining whether event-related potentials (ERPs) associated with goal-consistent memories change more across a night of sleep than ERPs associated with goal-irrelevant memories. Participants completed a memory task involving two sessions separated by a 24-hour delay. In the initial session, participants studied a series of images appearing in one of eight locations on a screen and their memory was immediately tested for the image locations. Half of the images were money-related (goal-relevant) while the other half were office supply (goal-irrelevant) images. After two study-test cycles were complete, each participant was informed that when they came back the next day they would complete one final memory test, and that if their memory for the locations associated with money images improved the following day, they would receive an extra five dollars. The instruction was meant to bias them by making the money-related images in line with their goal of increasing financial gains. ERP's were recorded for three time components (FN400, LPC, LFE) during the final test on day 1 (baseline) and the test on day 2 (delayed). Results revealed no difference in memory change from the baseline to the delayed test between the money-related and office supply images. However, ERP results revealed that there was a greater increase in the late positive component (500 – 800 ms) over the posterior regions from the baseline to the delayed test. This result suggests that memory for locations associated with money-related images may have been preferentially consolidated compared with office supply images. Additionally, the FN400 showed increased negativity at the delayed test compared to the baseline test over frontal regions, suggesting that familiarity increased over time for both image types. Finally, the LFE showed an increased positivity in the central ROI consistent with behavioral results suggesting that money-related images required more effortful processing to accurately retrieve.

1. INTRODUCTION

Declarative memory is the ability to consciously recall previously experienced facts and events, and is a central part of the human experience. Although most researchers would not disagree with its importance, there is still much debate about the ways declarative memory functions to maintain and adapt information over time. This thesis describes previous physiological, behavioral, and neuroimaging research that laid the foundation for the question of how the brain decides which memories to keep and maintain over the long term, and then describes a study conducted to examine how neural representations may be affected by this process.

Declarative memory is a unique form of long-term memory in that it requires the binding of multiple features into a coherent whole (Squire, 1992). For instance, when asked to recall dinner from last night, a person is combining information about the way the meal looked and tasted, the textures and smell, and the layout of the dinner table, as well as the conversations they had. This binding is accomplished via the hippocampus, which forms connections with different regions of the cortex, each specialized for processing different forms of information (Squire, 1992). Thus, this form of memory depends on multiple cortical regions for storage, such that the individual features are not enough to make up the memory. Instead the set of features must be linked together as one to establish the memory, which is initially accomplished via connections with the hippocampus (Paller, 1997).

Consolidation refers to the stabilization of long-term memories over time and occurs at both the cellular level as well as the systems level. Cellular-level consolidation, known as synaptic consolidation, is relatively rapid, done largely within a few hours but can take as little as a several minutes after encoding. The process involves changes in gene expression and related mechanisms of synaptic plasticity, involving the strengthening and/or weakening of synapses over time (Bramham & Messaoudi, 2005). Systems consolidation involves a restructuring of the brain regions involved in representing a memory. Systems consolidation necessarily involves changes at the cellular level, but with systems consolidation, it is those changes in the contributions of different brain regions that are highlighted (Frankland & Bontempi, 2005).

Prevailing Theory on Systems Consolidation

The prevailing theory regarding systems consolidation is known as the standard consolidation theory. This theory proposes that when new information is encoded, memory for the information becomes stored in hippocampal and cortical regions (Frankland & Bontempi, 2005). However, over time, recently learned information is reactivated both consciously and unconsciously, which serves to strengthen connections between different cortical areas involved representing the memory. As direct connections develop across cortical areas, the memory can eventually be accessed without a contribution from the hippocampus (Squire & Alvarez, 1995). This transfer process can potentially last for years until the memory becomes permanently stored in the cortex.

Researchers have used evidence from amnesic patients, who exhibit what is known as a temporal gradient, as support for this view. The idea is that patients with retrograde amnesia seem to have better recall for remote memories, meaning memories of things that happened a long time ago, as opposed to recent memories (Graham, Barense, & Lee, 2010). This finding fits nicely with the standard model of consolidation, as retrograde amnesics have damage to the hippocampus. Therefore, memories that have been fully consolidated and do not depend on a hippocampal contribution are easier to access and retrieve.

Systems consolidation is an active process and the exact duration likely depends on the frequency and nature of memory access during the time after encoding until retrieval. During the reactivation of a declarative memory, as the connections between bits of information being retrieved become more strongly bound together, they also become bound with related information (Paller, 2004). The strengthening of associations to related information gives the memory more neural pathways it can use when it is called upon in the future, making it more likely to be recalled each time. Although the standard theory is the dominant theory of how consolidation progresses over time, it should be noted that other possibilities also exist (e.g. multiple trace theory, Nadel & Moscovitch, 1997).

Sleep and Systems Consolidation

A fundamental aspect of memory encoding and memory consolidation is that both processes depend on the same networks in the brain, making the two operations difficult to do in concert. Therefore, sleep may provide the optimal time for systems consolidation to progress (Diekelmann & Born, 2010). Research has long shown that sleep facilitates the preservation of memories relative to a comparable period of waking (Jenkins & Dallenbach, 1924), but only recently has convincing evidence shown that processes actively occurring during sleep contribute to this preservation. For example, research with single-cell recordings in rodents observed the hippocampal firing patterns of neurons during learning and subsequent sleep and found that the patterns observed during learning are mimicked during sleep (Wilson & McNaughton, 1994). Also important is the finding that the proportion of reactivation of the hippocampal firing patterns is predictive of memory performance (Dupret, O'Neill, Pleydell-Bouverie & Csicsvari, 2010). Together, these studies show not only that memories are being accessed during sleep, but also that the frequency of access can be used to predict subsequent memory performance.

In humans, studies convincingly support the role of sleep in consolidation as well. One such study examined high school students' ability to remember English-German vocabulary lists. Results indicated that sleep following learning improved memory for vocabulary words relative to remaining awake after learning, and that sleep appears to be especially beneficial when it follows within a few hours after learning (Gais, Lucas, & Born, 2006). Plihal and Born (1997) found improved memory for word pairs following an interval of sleep when compared to an equal interval of wakefulness. Another study took these behavioral findings a step further by examining brain activity using fMRI. By testing face-location associations after a brief 15-minute delay period and 24-hour delay period (containing sleep) researchers demonstrated that changes in brain networks activated during memory retrieval could occur after just one night of sleep (Takashima et al., 2009). On the whole, these studies provide evidence that a period of sleep after learning improves memory recall, and are consistent with the idea that systems-level consolidation optimally progresses during sleep.

With much research concluding that sleep functions in part to facilitate systems consolidation, focus has shifted to determining what roles the individual stages of sleep have in stabilizing and enhancing memories. Electrophysiology is used to identify four different levels of sleep: stage 1, stage 2, slow-wave sleep (SWS), and rapid eye movement (REM). SWS has gained attention as a significant contributor to systems consolidation (Diekelmann & Born, 2010; Marshall & Born, 2007). One study, using regional measurements of cerebral blood flow in humans, showed that hippocampal areas that were active while learning a route in a virtual town were also active during a subsequent period of SWS. Additionally, the amount of hippocampal activation observed during SWS positively correlated with improvements in route retrieval the following day (Peigneux et al., 2004). Electroencephalographic (EEG) recordings show that during SWS, slow-oscillatory activity synchronizes firing patterns in neuronal populations (Dang-Vu et al., 2008). In rodents, a correlation between neuronal bursts in the cortex and hippocampus has been demonstrated, leading to speculation that slow waves can serve to coordinate information transfer between the cortex and hippocampus (Sirota et al., 2003).

While SWS may provide the sleeping brain with the necessary framework for hippocampal-neocortical communication, other research provides evidence for the role of sleep spindles (phasic oscillations that last between 1-3 seconds and range from 10-16 Hz) and REM sleep in transforming memories (Clemens, Fabo, Halasz, 2005). Clemens and colleagues (2005) measured verbal memory recall and counted spindles present during sleep. Their findings showed a correlation between the number of spindles and memory retention, suggesting that spindles also play a role in overnight consolidation processes. Other studies that have examined relationships between memory and sleep spindles have found similar results (Schmidt et al., 2006; Schabus et al., 2004). Research focused on REM sleep has primarily implicated REM in the consolidation of procedural memories (Kuriyama et al., 2004) and in the processing of emotional declarative memories (Stickgold et al., 2001).

Although much more information about the role of sleep and the various stages in memory consolidation have come to light in recent decades, one big question that still remains is in regard to why some memories are strengthened via consolidation, whereas others are forgotten. Much more research is needed to determine exactly what processes are involved in the selection of certain memories over others.

The Selectivity of Memory Consolidation

Research on the selectivity of memory consolidation is beginning to provide evidence that sleep can act as a filter, facilitating the stabilization of certain types of memories; including emotional stimuli over neutral stimuli, object-location pairs related to high monetary rewards compared with low monetary rewards, and retrieval expectancy, or information expected to be of future relevance (Payne, Stickgold, et al., 2008; Oudiette et al., 2013; Wilhelm, Diekelmann, et al., 2011; van Dongen, et al., 2012). The results of these studies illustrate not only how consolidation benefits from sleep compared to a period of wake, but also that information believed to be relevant for future utilization seems to be preferentially accessed during sleep (Walker & Stickgold, 2013). For example, when participants were told after learning word-pair associates that their memories for the word pairs would be subsequently tested after sleep, they remembered more than those who were not told about the test (Wilhelm, Diekelmann, et al., 2011). Similarly, Van Dongen and colleagues (2012) had subjects learn two sets of picture-location associations and then told them that only one would be tested the following day. The next day they tested students on both sets and found that the post-learning instruction regarding the relevance of certain picture-location associations selectively improved recall performance only when the delay contained sleep. The sleep-dependent improvements in retention were not seen for the picture-location set that was perceived as irrelevant (van Dongen, et al., 2012). This evidence supports the belief that sleep is beneficial for memory retention when the information is expected to be of use in the future. In another set of experiments, researchers had participants learn object-location associations that were manipulated to be of high or low -value, denoted by a number on each object that corresponded to the value of a potential reward that could be earned at future recall. Each object was paired with a characteristic sound during learning and at recall (dog + bark). Memory was tested after either a 90-minute nap or an equal period awake, and researchers found that regardless of wake or sleep, memory was better for objects related to high values compared with low value objects. Additionally, when sounds were used to reactivate memories during sleep all of the low-value objects were rescued from forgetting, while only cued objects were rescued from forgetting when sounds were used to reactivate memories during sleep. Those findings provide evidence that sleep benefits memory retention for information associated with high values, and that sleep may play a role in connecting related information through targeted reactivation (Oudiette et al., 2013).

In summation, we know that processing that takes place after initial acquisition results in changes in declarative memories over time. These changes occur due to repeated activation of the memory and result in stronger connections across the cortex, and this process is facilitated during slow-wave sleep, In addition, this process is selective. It has been suggested that memories may be consolidated to the extent that they are deemed useful for future events, and recent research support this view. Although demonstrating that memory is better for goal-relevant than for other information following sleep is encouraging, more powerful support for this theory is necessary.

Event-Related Potentials

Event-Related potentials (ERPs) are electrical potentials produced by the brain in response to a stimulus. ERPs are computed from ongoing electroencephalographic (EEG) data recorded at the scalp, are used to index a variety of emotional and cognitive processes, and are time locked to a particular event. An ERP component is a positive or negative voltage deflection that occurs at a particular time in response to an event and is related to a specific cognitive, perceptual or motor process (Luck, 2014). Many ERP components are named based on the positive or negative voltage fluctuation they are associated with, the region in which those deflections are observed, their onset latency, or some combination of the three. For example, the FN400 ERP component is a frontally located event with a negative voltage fluctuation that onsets around 400 ms.

Declarative memory is typically associated with three distinct ERP components. The FN400 is an increased negativity that onsets around 400 ms and is observed over frontal recording sites. The late positive component (LPC) is typically present between 500-800 ms, and is an increased positivity over parietal recording sites. The LPC and FN400 are thought to index recollection and familiarity, respectively (Rugg & Curran, 2007). Recollection reflects conscious recall of an event that involves contextual details, such as where or when an event was experienced, while familiarity is thought to reflect a simple “feeling of knowing” that something occurred and doesn’t include contextual details (Tulving, 1985). A final component, the late frontal effect (LFE), is a late (800ms-1200ms) positivity that is maximal over frontal sites and is thought to reflect post-retrieval monitoring processes (Curran, Schacter, Johnson, & Spinks, 2001) or retrieval effort (Ally & Budson, 2007).

ERP's have seldom been used to examine how memory representations change across time and/or sleep, although a few recent studies have begun to shed light on the issue. In one recent study, participants studied unfamiliar faces prior to a retention interval filled with either wake or sleep, which was followed by a recognition test where participants were required to determine whether the face was had been seen before or was new. ERPs were recorded during the recognition test and results indicated that the amplitude of the LPC was larger in the group that slept during the delay than for the group that remained awake, indicating that recollection became stronger after a period of sleep (Mograss et al., 2006). Results from a later study using the same paradigm replicated those findings and showed that sleep primarily influences accuracy, supporting the idea that consolidation focuses on reorganizing weak associations in a way that strengthens the networks associated with them. In both studies, sleep had no influence on the FN400, suggesting that familiarity is unaffected by consolidation processes during sleep, and is consistent with the results of Atienza and Cantero (2008) who found no effect of sleep on behavioral measures of familiarity. In addition, their finding that the LFE was larger after sleep than wake shows that sleep may help influence effortful context integration (Mograss et al., 2008).

In another recent study, investigators used ERPs to examine changes in brain activity for familiar and newly learned words after a period of consolidation (Palmer et al., 2013). In a two-day study, recognition memory for familiar and novel words was assessed 45 minutes after training on the first day, and then again on the second day without any additional training. Investigators found that for both familiar and novel words, the late positive component (LPC), distinguished old items from new items on both days. For trained familiar words, the LPC became weaker on day two, but for trained novel words, the LPC was significantly greater on the second day. The finding shows that recollection for familiar items fades over time, but recollection for novel items becomes better after a period of consolidation. The results of these studies suggest that ERPs can be an effective way of showing how memory representations change after a period of consolidation.

Purpose of the Current Study

In the current study, ERPs were used to determine if larger changes in the LPC would be observed for goal-consistent memories than for other, goal-irrelevant memories, to further test the hypothesis that consolidation favors information that is in line with our future goals. The present study modified the paradigm used by van Dongen and colleagues (2012). Rather than instructing participants that only one set of objects would be tested at session 2, participants were informed that they would be tested on both types image types again but that they could earn a larger monetary reward be remembering more of a certain set of images (money-related) the next day than at they did at session 1. Money related images were used as a category here (versus office supply images) to heighten the distinction between goal-relevant and goal-irrelevant images such that money should be a more inherently goal-relevant image type. The FN400 was examined, but no differences were expected in the FN400 across time, given prior studies found no effect on this component (Mograss et al., 2006; Mograss et al., 2008; Palmer et al., 2013).

The LFE was of interest here because if one image type is more strongly consolidated, for correctly remembered images, a greater positivity would be expected for the less strongly consolidated images, reflecting increased retrieval effort and/or post-retrieval verification and monitoring.

2. METHOD

This study was reviewed and approved by the Texas State Institutional Review Board (IRB).

Participants

Thirteen students, 10 women and 3 men, from Texas State University ranging in age from 18-25 years (mean: 19.8 years, SD: 2.7) were tested. Participants were recruited through announcements made in psychology courses and compensation for completing the two-session study was $20-$25. Participants were guaranteed to earn $20 with the potential to earn an extra $5 based on memory performance (see below). Exclusion criteria included use of prescription sleep medications, a previously diagnosed sleep disorder, and left-handedness. In the present study all participants were right handed and no use of prescription sleep medications or previously diagnosed sleep disorders were reported. Data from one participant was excluded due to extremely low memory performance (greater than 2.5 standard deviations below the mean).

Materials

A total of 120 images were used. Half of the images were pictures of money-related items such as dollar bills, coins, and symbols (e.g., ¢, $) and the other half of the images were of office supplies (e.g., stapler, ruler, etc.). All images were placed on a white background and were sized equally at 266 x 281 pixels.

Procedure

The experiment was conducted in two sessions, with a 24-hour delay between sessions. Upon their arrival to the first session, participants were given the Pittsburgh

Sleep Quality Index (PSQI; Buysse et al., 1989) to ensure participants had normal sleep habits and quality over the past month. Next, participants completed the Edinburgh Handedness Inventory to assess handedness (mean=.69, where 0 = ambidextrous, -1 = completely left-handed, 1 = completely right-handed; Oldfield, 1971). Informed consent was then obtained from eligible participants. Each participant then completed the Karolinska Sleep Log (KSL) survey regarding sleep quality during the past 24 hours (Akerstedt et al., 1994), and were then prepped for the EEG recording.

Next, participants were seated at a computer, approximately 112 cm from the monitor and viewed 120 pictures of objects one at a time for 4 s each, in 1 of 8 possible locations on the screen. Half of the objects were money-related and the other half depicted office supplies. The order of presentation was random and the location of presentation was counterbalanced across stimuli using the “random presentation” setting in the E-Prime software suite (Pittsburgh, PA.). In order to minimize distractions and maintain attention, fifteen filler trials in which a solid red rectangle appeared in the middle of the screen and participants were instructed to press the ”1” key each time it appeared were randomly intermixed with the experimental trials. Immediately following study of all 120 images, participants took a memory test for the previously studied picture locations. Each studied item appeared one after another in the center of the screen, in a random order, and participants were asked to select which of the eight areas on the screen the image appeared in during the study phase by pressing the corresponding number on the keyboard. The images remained on the screen until the participants made a selection. No new images were present on the test.

Session one involved two encoding/retrieval cycles. During the second encoding phase, the images were shown in the same locations but in a different random order. During the second test phase, trials were presented in a different random order at the center of the screen. At the conclusion of the second retrieval phase, participants were told that they would receive an extra $5 if they could remember more of the money-related image locations the following day than they did during the final test of session one (the baseline memory test). This instruction was meant to bias them to more strongly consolidate the locations of the money-related images compared with the office supply images during the intervening night of sleep.

The following day participants returned to the lab for session 2, completed the KSL (with regard to the intervening night), and were prepped for the EEG recording. Next, they took one final memory test for the image locations that was identical to the tests completed the previous day, with the exception that images appeared in a different random order. This test is henceforth referred to as the delayed test. Data from one participant was excluded due to extremely low memory performance.

Behavioral Analyses

Memory accuracy for the image locations was compared using a 2x2 repeated measures analysis of variance (ANOVA), with test (baseline, delayed) and image type (money, office supplies) as the within-subjects independent variables and percent correct as the dependent variable. If information consistent with future goals is preferentially consolidated across a delay, then a significant test x image type interaction should be present, such that memory for image locations will improve to a greater extent from the baseline test to the delayed test for money-related images compared with other images.

Electrophysiology Procedure and Analyses

For both sessions of the experiment, EEG data was recorded using an ActiveTwo biopotential measurement system. The system employs an assembly of 64 active electrodes that are connected to a cap in addition to electrodes placed above and below the left eye as well as on the temple, or outer canthus, of both eyes. The electrical activity was collected with a sampling rate of 256 Hz and amplified with a bandwidth of 0.03-100 Hz. Recordings were referenced to a common average reference to reduce the amount of activity added by the required reference electrode. EEG signals were recorded with respect to a common mode sense active electrode placed between the PO3 and POz channels, then re-referenced offline to the average of that reference (Murray, Brunet, & Michel, 2008). The range of the signal offsets for all participants were within +/- 50mV.

Using the EMSE Software Suite (Source Signal Imaging), data were corrected for excessive eye movements. Artifact data were manually identified using the empirical EMSE Ocular Artifact Correction tool wherein a ratio of artifact data to clean data was developed and ocular artifacts removed from the appropriate channels. Trials were removed from analyses if they had baseline drift or movement greater than 90 μV using the EMSE spatial interpolation filter. Bad channels were manually identified and corrected using the EMSE suite artifact correction algorithm. With this algorithm, artifact (bad) segments of data are manually selected and labeled as such, then clean segments of data are manually selected and labeled. The EMSE suite program then creates a filter that subtracts all of the artifact data from the channels where it is detected (Pflieger, 2001).

ERPs were then computed at each electrode by taking the average amplitude across three time windows corresponding to three commonly observed effects in the memory literature (FN400: 300-500 ms, LPC: 500-800ms, and LFE: 800-1200ms) for each experimental condition (baseline money, baseline office supplies, delayed money, delayed office supplies). These ERPs were created with respect to test stimuli presented at central fixation. ERPs for each condition and component at each electrode were then averaged across four regions of interest (ROIs). The FN400 was examined over the right anterior (af7, af3, f7, f5, f3, fc5 and fc3) and left anterior regions (af4, af8, f4, f6, f8, fc4, fc6 and ft8) regions, the LFE was examined over the central region (fpz, afz, fz, fcz, f1 and f1) and the LPC was defined over the posterior region (cp1, cpz, cp2, cp4, p5, p3, p1, pz, p2, p4, p6, po3, poz, po4, po8, o1, oz and o2; see Figure 1). The number of valid trials per condition remaining after artifact correction varied by individual (Table 1), but was always greater than 16 the average number of valid trials per participant was 34.6 (SD=13).

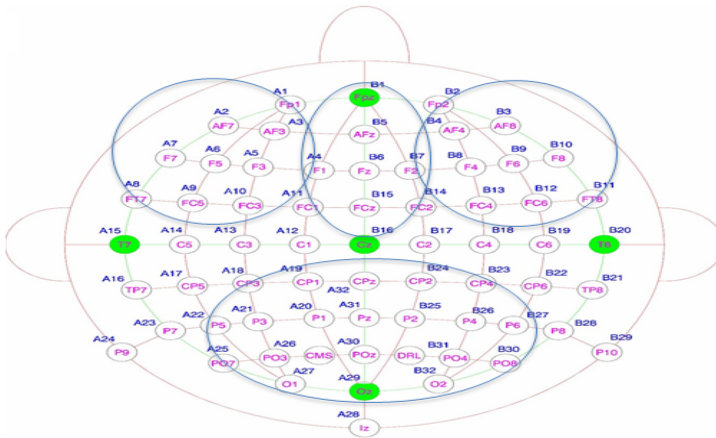

Figure 1. Regions of Interest and the channels that comprised them. From left to right: anterior right, central, anterior left, and posterior at the bottom

For the FN400 component, a 2x2x2 ANOVA was conducted with test (baseline, delayed), image type (money, office) and ROI (anterior left, anterior right, central and posterior) as within-subjects variables, and mean amplitude for hits (correct responses) as the dependent variable. For the LFE and LPC components, 2x2 ANOVAs were conducted with test (baseline, delayed) and image type (money, office) as within-subjects variables and mean amplitude for hits as the dependent variable. If money-related images gained preferential access to consolidation processes compared with office supply images, it is expected that the LPC component would show a test x image type interaction, based on results from previous investigations (Rugg & Curran 2007), reflecting differential changes in the ability to recollect image locations for money images compared with office supply images. No strong hypotheses regarding whether the FN400 and LFE would show effects were generated. If present, the FN400 could be expected to show no difference from baseline to delay based on the prior literature (Mograss et al., 2006; Atienza & Cantero, 2008; Mograss et al., 2008). The LFE, however, may be larger for office supply images than for money-related images, reflecting greater retrieval effort for those goal-irrelevant stimuli.

Subject	**Baseline Money**	**Baseline Office**	**Delayed Money**	**Delayed Office**
1	22	25	32	30
2	22	18	19	24
3	38	39	30	33
4	46	49	40	45
5	54	54	53	56
6	58	58	53	55
7	33	30	17	18
8	28	28	23	23
9	53	49	21	23
10	28	36	24	24
11	44	48	33	37
12	25	26	16	20

Table 1. Total number of valid trials per subject, per condition.

Sleep Data Analyses

Data collected via the KSL, for the night prior to session 1 as well as the intervening night between sessions 1 and 2, was used to determine the average amount of time that elapsed between session 1 and sleep onset, and the average sleep time during the intervening night. Other measures were also calculated in order to track self-reported assessments of sleep quality prior to each session, these included rating how each participant slept, how refreshed they felt after sleeping, and how soundly they slept (See Appendix B for full questionnaire). For each measure, group averages were calculated for both nights.

3. RESULTS

Behavior

A 2x2 repeated measures ANOVA was conducted with test (baseline, delayed) and image type (money, office) as the within-subject independent variables and proportion hits as the dependent variable. There was a significant main effect of test $F(1, 11)= 33.0$, $p<.05$, indicating that for both image types, memory was more accurate for the baseline test (75.3%) compared with the delayed test (63.3%). The main effect of image type was marginally significant $F(1, 11)=4.4$, $p=.059$, indicating that memory for office supply image locations (71.4%) was slightly more accurate compared with money image locations (67.1%). The test x image type interaction failed to reach significance (p value > .3; Figure 1).

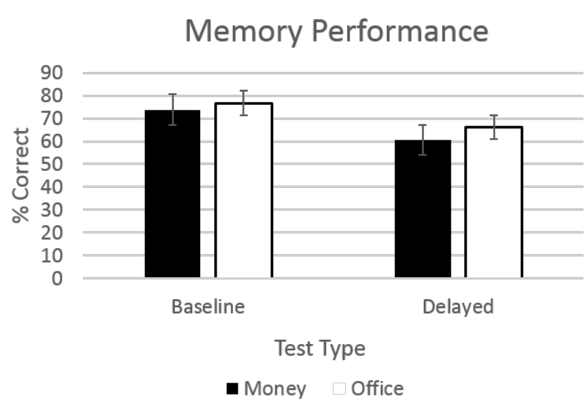

Figure 2. Percent of correctly identified object locations as a function of test (baseline, delayed) and image type (money, office). Bars indicate standard error of the mean.

Sleep Measures

The average amount of time slept prior to session 1 was 7.1 hours (SD= 2.0 hours), prior to session 2 participants reported sleeping an average of 7.9 hours (SD=.1.4 hours). When asked to rate how they slept (1-5; very poorly-very well), prior to session 1 participants averaged a response score of 3.6 (SD=.8). Prior to session 2 participants averaged a response score of 3.8 (SD=.94). Prior to session 1 when participants rated if they felt refreshed after waking (1-5; not at all-completely) the average response was 2.8 (SD=1.2), prior to session 2 the average response was 3.6 (SD=1). Finally, when participants reported how soundly they slept (1-5; very restless-very soundly) prior to session 1 the average response score was 3.5 (SD=1), prior 2 session to the score was 3.9 (SD=.9). Participants took an average of 25.9 minutes to fall asleep prior to session 1 (SD=20.6), and an average of 20.6 minutes to fall asleep prior to session 2 (SD=20.4). Participants reported an average of 1.3 awakenings the night prior to session 1 (SD=1.5) and an average of .8 awakenings the night prior to session 2 (SD=1.1). Participants who had an awakening on the night prior to session one were awake for an average of 26.3 minutes (SD=31.9), and were awake for an average of 19.4 minutes if they had an awakening the night prior to session 2 (SD=17.7). It should be noted that one participant was awake for 90 minutes after falling asleep the evening prior to session 1, and 45 minutes the evening prior to session 2. When asked if they slept throughout the time allotted for sleep (1-5; woke up too early, slept through the night) participants averaged a response score of 3.3 for the night prior to session 1 (SD=1.3), and 4.3 for the night prior to session 2 (SD=1). When asked how easy it was to wake up (1-5; very easy-very difficult), for the night prior to session 1 participants averaged a response score of 2.8 (SD=1.3), and for the night prior to session 2 participants averaged a response score of 2.5 (SD=.9). When asked how easy it was to fall asleep (1-5; very easy-very difficult), participants reported an average response score of 2.3 (SD=1.4) for the night prior to session 1 and an average score of 2.2 (SD=1.2) for the night prior to session 2. Finally, when asked how much they dreamt last night (1-5; none-much), participants reported an average response score of 2.2 for the night prior to session 1 (SD=1.1), and 2.1 for the night prior to session 2 (SD=.8). Taken as a whole, the KSL data suggests that

Event-Related Potentials

Two 2x2 repeated measures ANOVAs were conducted for the LPC and LFE components, respectively with test (baseline, delayed) and image type (money, office) as within-subjects independent variables and mean amplitudes for hits (correct responses) as the dependent variables, while a 2x2x2 repeated measures ANOVA was conducted for the FN400 with test (baseline, delayed), image type (money, office), and ROI (anterior left, anterior right) as within-subjects independent variables and mean amplitudes of hits (correct responses) as the dependent variable.

For the LPC component, there were no significant main effects or interactions observed after conducting the 2x2 ANOVA, (*p* values >.1). To test the a priori hypothesis that a larger change in amplitude would be observed from the baseline test to the delayed test for the money images, change scores were computed by subtracting the mean amplitude for the baseline test from the mean amplitude for the delayed test for each image type. Numerically, amplitude for money images changed to a greater extent (1.8 μV) than amplitude for office supply images (-.01 μV) from the baseline to the delayed test, although a paired samples *t*-test revealed that the change did not reach significance $t(11)=1.7$, $p=.11$. Despite not reaching significance, the increase in the LPC is consistent with the predictions of the present study in that it suggests that recollection increased for money-related images over time and decreased slightly for office supply images, as evidenced by the increased positivity from baseline to delayed test for money-related images, and the decreased positivity from baseline to delayed test for office supplies, illustrating the selective nature of consolidation (Figure 3a & b).

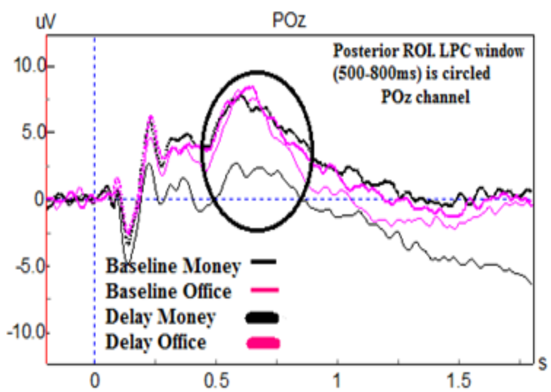

Figure 3a. Waveforms depicting the increased LPC ERP for money-related images from baseline (black, thin) to delayed (black, thick), and the very slight decrease in amplitude for office from baseline (pink, thin) to delayed (pink, thick)

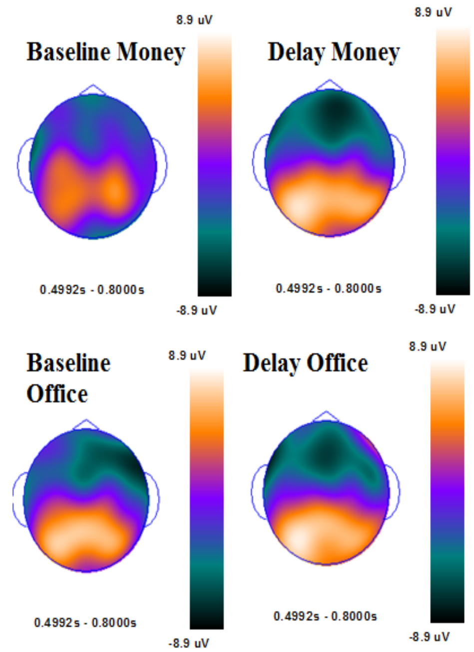

Figure 3b. Topographic maps in the LPC time window showing change in electrical activity at the posterior region over time.

The 2x2x2 ANOVA for the FN400 component revealed a marginally significant main effect of test, *F*(1, 11)=4.1, *p*=.068, reflecting more negative mean amplitudes at the delayed test (-3.6 µV) than at the baseline test (-2.6 µV) in the anterior left and right ROIs (Figure 4). Although no changes were expected for the FN400 component, this finding suggests that familiarity increases over time. There was also a marginally significant interaction between test and image type, *F*(1, 11)=3.8, *p*=.076. Change in mean amplitudes from baseline to delayed test was then computed for

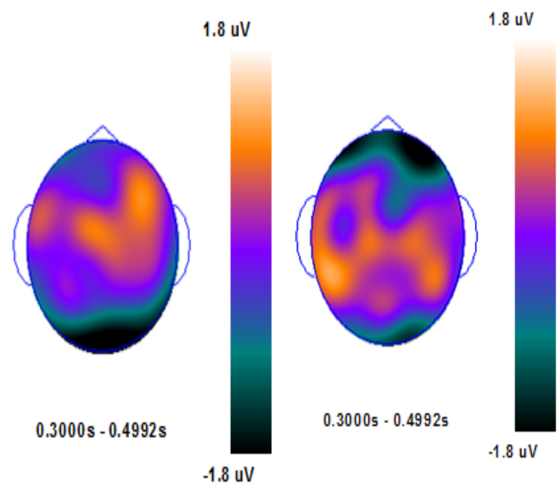

Figure 4. FN400 component showing increased negativity at delayed (right) than at baseline (left) in the anterior left and right ROIs

both image types. A numerically greater change in mean amplitudes for money (1.6 μV) than for office (.4 μV) was observed, a paired *t*-test was done to investigate if the change was significant and the results revealed a marginally significant difference in the change in mean amplitudes for money-related and office supply images from the baseline to the delayed test $t(11)=-2.0$, $p=.051$, (Figure 5). No other main effects or interactions were significant (p values > .1).

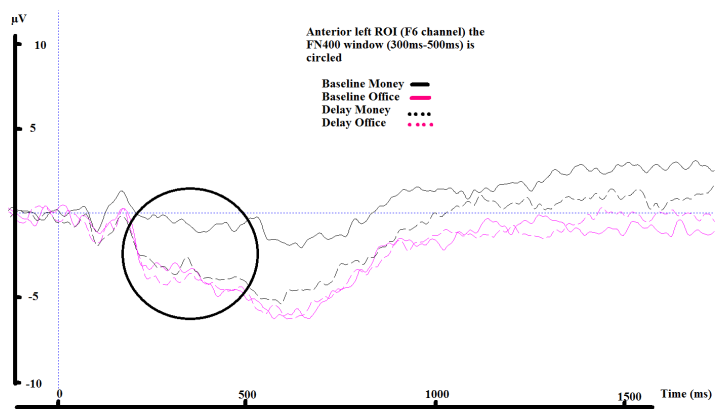

Figure 5. Waveforms for each condition and image type for the FN400 component

The 2x2 ANOVA for the LFE showed a significant main effect of image type $F(1, 11)=11.6$, $p<.01$, reflecting more positive amplitudes for money images (-4.5 μV) compared with office-related images (-5.7 μV) (Figure 6). This suggests that even for correctly remembered images, money-related images required more effortful processing than office supply images. No other main effects or interactions were observed (p values >.3).

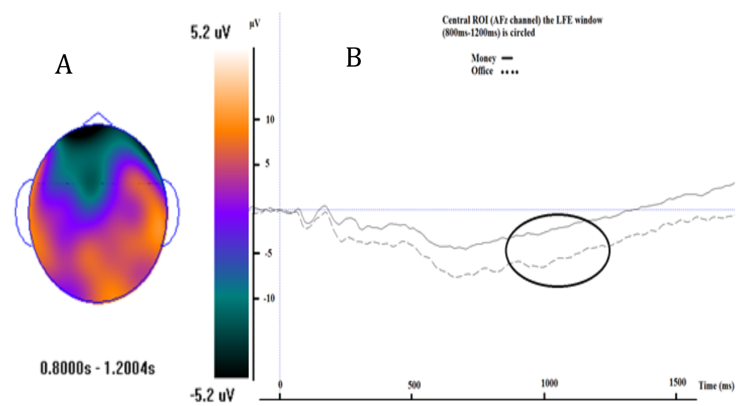

Figure 6. A) LFE component, difference in amplitudes between money and office related images showing greater positivity for money-related images in the central ROI. B). Difference in mean amplitudes between money (solid) and office-related (dashed) images for the LFE component (circled) at the AFz channel in the central ROI.

4. DISCUSSION

The present study investigated whether money-related images were preferentially consolidated across a 24-hour delay compared with office-supply images. It was hypothesized that memory performance for money-related images would improve to a greater extent, given that money images may be inherently more incentivizing and that participants were given the added incentive of earning an extra $5 if they could remember more money-related image locations on the delayed test compared with the baseline test. No such incentive was given for remembering the locations of the office-supply images on the delayed test. Behaviorally, the change in memory from the baseline to the delayed test was equivalent for money-related and office supply images. However, the ERP results indicated that the LPC over the posterior ROI numerically increased to a greater extent across the delay period for money-related images compared with office-supply images, suggesting a preferential strengthening of memories for the locations of the memory-related images over time.

It is thought that the LPC over parietal regions is an index of recollection (Rugg & Curran, 2007), and previous results have demonstrated that the parietal LPC is strengthened across a consolidation period (Mograss et al., 2008; Palmer et al., 2013). Consistent with this finding, in the posterior ROI, the increase in the LPC from the baseline to the delayed test was numerically (but not significantly) greater for money-related images compared with office related images, suggesting that in that region, consolidation processing may have strengthened memory for money-related image locations to a greater extent than memory for office-supply image locations. Although the selective consolidation of memories has previously been demonstrated through behavioral enhancements for some but not all memories after a delay, this is the first demonstration that the ERP correlates of memory representations can be differentially affected by a consolidation period.

Presumably, the selective strengthening of money-related image locations occurred during sleep (e.g., Stickgold & Walker, 2013). One study examining the effects of sleep on recall of paired-associate lists found that, compared with those who remained awake after learning, the participants who slept had significantly better recall (Plihal & Born, 1997), while in another study researchers found that compared to being awake after learning, post-encoding sleep can selectively enhance recall for items cued to be remembered and selectively ignore information for items cued to be forgotten at learning, illustrating how selectivity can be manipulated by instructions given prior to sleep (Saletin et al., 2011). In the present experiment, participants slept an average of 7.1 hours the night before their initial arrival on day 1, and an average of 7.9 hours the night between the baseline and delayed tests. Whether the changes in ERPs reported here depend on sleep per se is currently unknown, but it should be explored in future research.

Although the LPC findings are consistent with the hypothesis that memory consolidation can be selective, no such support was found in the analyses of memory performance. One reason no differences in memory change between money-related and office-supply images were observed in behavior, and why the LPC effect did not reach significance could simply be a lack of power. With only 12 participants, modest differences in memory may not have been strong enough to lead to a significant difference. Prior studies examining sleep and memory consolidation have collected data from more participants, Plihal and Born used 20 in their 1997 study, while van Dongen and colleagues (2012) tested 60 participants, suggesting that a substantially greater number of participants may be necessary to find recall effects.

Despite no differences in memory change across the delay for money-related versus office-supply image locations, collapsed across test, memory for office-supply image locations was marginally greater than memory for money-related image locations. This may have occurred because office-supply images tended to be more distinct from, and diverse than the money-related images. If the features of the office-supply images make them more recognizable and less similar to one another compared with than money-related images (which were on average less colorful and several included United States currency), then potentially memories for office-supply image locations may have been slightly stronger due to the more distinctive nature of those images. Prior literature has shown that memory for an event can be influenced by how different the event is from others that need to be distinguished at the time of retrieval (Surprenant, & Neath, 2009).

In addition to the LPC effects, ERP effects were also observed in the FN400 and LFE time windows. The FN400 is exhibited as an increased negativity at frontal recording sites and has previously been associated with the memory experience of familiarity, which is thought of as memory for a previous experience without contextual details, and is indicative of a simple feeling of knowing that something was seen, but not necessarily in what context (Yonelinas, 2001). Here, regardless of image type, at frontal ROIs, the FN400 was stronger for the delayed test compared with the baseline test. This finding suggests that over time, familiarity for the images increased. However, a marginally significant difference in the strengthening of the FN400 was observed between image types from the baseline test to the delayed test reflecting a greater increase of the FN400 for money-related images as opposed to office supply images. This is the first time an increase in familiarity has been observed after sleep, which could be due to increased fluency with the objects. This might be expected with the current study paradigm because participants experienced an additional exposure to the stimuli at the delayed test compared with the baseline test, and prior recognition memory research has shown that repeated exposure to certain stimuli can manifest as a later feeling of familiarity (Jacoby & Dallas, 1981).

The LFE ERP component is believed to be indicative of post-retrieval monitoring processes such as continued evaluation of contextual features. In prior research the LFE was found to be maximal when participants made correct judgements as to whether they had seen the stimuli before, and if so, what the source (context) of the stimuli was, compared with when participants only made judgments about whether the stimuli had been presented before (Wilding & Rugg, 1996). Those findings indicated that the LFE component is more pronounced when the successful retrieval of information requires more effort, such as making additional evaluations of contextual details. In the present experiment, the LFE was stronger for money-related images compared with office-supply images. This suggests that the retrieval of money-related image locations was more effortful, and/or required greater monitoring of the retrieved information, which may be expected if memories for money-related image locations were initially weaker than memories for office-supply image locations (as was observed here).

The present study has three additional limitations. One is that there was a large time period (an average of 11.75 hours) that elapsed after session 1 and before sleep.

Previous research has shown that sleep is most beneficial to memory consolidation when it occurs within a few hours of learning (Gais, Lucas, & Born, 2006). Thus, sleep-dependent consolidation processes may not have been as effective here as they might have been if participants were allowed to sleep immediately after learning. A second limitation is that the post-encoding instruction, wherein participants were told they could earn an extra $5 if they could remember more money-related image locations the following day, may not have been motivating enough to bias the selective consolidation of money-related images. Although past research has demonstrated that information associated with monetary rewards is preferentially consolidated, it is possible that the fiscal reward was simply too small to become relevant. Additionally, this instruction was not counterbalanced across stimuli so it is unknown if the instruction would have had a different impact on memory performance had it been given for the office supply images as well. Future research could further investigate consolidation of goal relevant information over time by addressing these limitations, specifically the time period between learning and sleep.

In summary, the current results provide a novel look at potential ERP correlates of memory consolidation. In particular, the LPC showed a numerically greater increase for money-related images compared with office supply images, suggesting that memory representations for money-related images underwent more extensive processing across time compared with office-related images. It is expected that this difference would be significant with additional power. In addition, familiarity for all images appears to increase over time, as evidenced by the increased FN400 and, as evidenced by the poor recall performance at the delayed test, this may reflect increased fluency with objects at the delayed test compared with the baseline test. Furthermore, the LFE showed more positivity for money-related images compared with office supply images. The finding suggests that more effortful processing may have been required to accurately recall image locations for the money-related images and is supported by the decreased recall accuracy for money-related images compared with office supply images.

APPENDIX SECTION

APPENDIX A: PITTSBURGH SLEEP QUALITY INDEX (PSQI)

Instructions: The following questions relate to your usual sleep habits during the past month *only*.
Your answers should indicate the most accurate reply for the *majority* of days and nights in the past month. Please answer all questions.

	Not during the past month	Once a week	Twice a week	Three times a week or more
1. During the past month, how often have you had trouble sleeping because you…				
a. cannot get to sleep within 30 minutes				
b. wake up in the middle of the night or early morning				
c. have to get up to use the bathroom				
d. cannot breathe comfortably				
e. cough or snore loudly				
f. feel too cold				
g. feel too hot				
h. have bad dreams				
i. have pain				
j. other reason(s) for poor sleep, please describe here:				

2. During the past month, how often have you taken medicine (either prescription or “over the counter”) to help you sleep?

3. During the past month, how often have you had trouble staying awake while driving, eating meals, or engaging in social activity?

4. During the past month, how would you rate your sleep quality overall?

Very Good   Fairly Good   Fairly Bad   Very Bad

5. During the past month, how much of a problem has it been for you to keep up enough enthusiasm to get things done?

No problem at all	Only a very slight problem	Somewhat of a problem	A very big problem

6. During the past month:

a) What time have you usually gone to bed at night?

USUAL BED TIME ______________________________

____

____

b) How long (in minutes) has it usually taken you to fall asleep each night?
NUMBER OF MINUTES ______________________________

c) When have you usually gotten up in the morning?

USUAL WAKE UP TIME ______________________________

____

____

d) How many hours of *actual sleep* did you get at night?
HOURS OF SLEEP PER NIGHT ___________________________________

____

(This may be different than the number of hours you spend in bed.)

APPENDIX B: KAROLINSKA SLEEP LOG (KSL)

KAROLINSKA SLEEP LOG Date:___________________

1. At what time did you go to bed and turn the light off last night? ___________PM or AM
2. At what time did you arise this morning? ___________PM or AM
3. How long did you sleep? ___________hours and ___________minutes
4. How long did it take you to fall asleep? ___________hours and ___________minutes
5. How many awakenings did you have last night? ___________
6. How many total minutes were you awake after falling asleep last night?

__________minutes

(Don't include time in bed before falling asleep)

Circle one per question only:

7. How did you sleep?

1 2 3 4 5

Very Poorly Very Well

8. Did you feel refreshed after you arose this morning?

1 2 3 4 5

Not at all Completely

9. Did you sleep soundly?

1 2 3 4 5

Very Restless Very Soundly

10. Did you sleep throughout the time allotted for sleep?

1 2 3 4
5

Woke up much too early Slept thru
the night

11. How easy was it for you to wake up?

1 2 3 4
5

Very Easy Very
Difficult

12. How easy was it for you to fall asleep?

1 2 3 4
5

Very Easy Very
Difficult

13. How much did you dream last night?

1 2 3 4
5

None
Much

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