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Reconsolidating: The Effect of Spatial Context and Expectations

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RECONSOLIDATION: THE EFFECTS OF SPATIAL CONTEXT AND EXPECTATIONS

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ABSTRACT

Consolidation is the process by which memories become stable over time. Accessing a previously consolidated memory trace brings it back into a labile state where it must then undergo a re-stabilization process known as reconsolidation. During this process memories are again susceptible to interference and may be updated with new information. Reconsolidation has been demonstrated in animals as well as in the procedural and episodic human memory systems. The exact boundary conditions for reconsolidation are not yet known. Some studies suggest that reconsolidation is only necessary when new information is presented in a spatial context that is indistinguishable from the spatial context of the original memory, indicating that spatial context alone has the properties required to reinstate the context of the original learning. Other recent results indicate that regardless of space, reconsolidation is used as an updating mechanism that is only required when there is a mismatch between original and new learning. Here, I provide further evidence that spatial context plays an important role in triggering reconsolidation, and that a single salient cue is unable to do so (Experiment 1). However, if spatial context is not varied, it may be the case that prediction error can be used to create a need for memory updating via a reconsolidation process (Experiment 2).

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CHAPTER 1

INTRODUCTION

Most memories become more stable over time during a process known as consolidation. A newly acquired memory is in a more labile state because it has yet to complete the consolidation process and is therefore more susceptible to change than an older one. However it may be necessary for older memories to be updated with newer information. The reconsolidation hypothesis suggests that a memory trace that is activated must be re-stabilized during a process known as reconsolidation. That is, activating an older memory can bring it back into a labile state. Once a memory trace is accessed and brought into a labile state, it can be strengthened, impaired, or altered. Previous to reconsolidation research it was thought that memories would start and stop the consolidation process only once. New evidence suggests that memories can be altered, even if they have been fully consolidated. The goal of this study is to further identify the specific boundary conditions of reconsolidation, while evaluating some of the existing theories.

CHAPTER 2

REVIEW OF RELATED LITERATURE

Reconsolidation in Animals

Just like consolidation, development of the theory of reconsolidation began in rat models. Schiller and Phelps (2011) identified three criteria that must be met to establish evidence for reconsolidation. First, the memory in question must be reactivated. Second, there must be some kind of treatment administered which is designed to alter the memory post-activation. In the current literature, this ranges from the presentation of interfering information to a pharmacological blockade of reconsolidation (Dudai & Eisenberg, 2004). Lastly, a memory test is administered to determine if reconsolidation has taken place. In the animal literature, treatment effects impair the original memory and as a result the memory is weakened or lost. A typical animal paradigm in the reconsolidation literature has the following components: first, a study maze or association is learned; second, a reminder of the original learning is given, (this is usually done by exposing rats to a conditioned stimulus that serves only as a reminder), followed by either a drug known to interrupt reconsolidation, or a placebo; finally, the memory test reveals if the treatment was successful in blocking or interrupting the reconsolidation process or not. If reconsolidation was blocked, there will be damage to the original learning so that animals that received the treatment show impaired performance as compared to those in the placebo condition (see Figure 1).

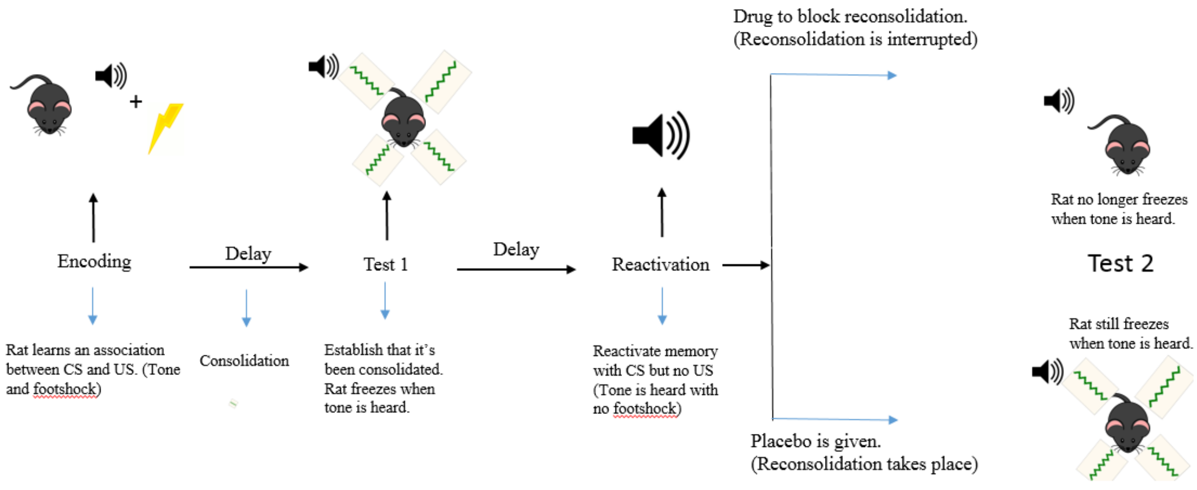


Figure 1: Standard animal reconsolidation paradigm

In the first study demonstrating reconsolidation effects, rats showed a decrement in fear memory when a brief reminder was presented and followed by an electroconvulsive shock (ECS), a treatment known to cause amnestic effects when applied in early stages of consolidation (Misanin, Miller, & Lewis, 1968); this effect was first termed cue-dependent amnesia. The research that followed was dedicated toward replicating and exploring this phenomenon. Bregman, Nicholas, and Lewis (1976) found that rats that were given an electroconvulsive shock at the starting point of a previously learned maze experienced an amnesic effect and could no longer complete the maze without errors. Memory for the maze remained impaired on all subsequent attempts. Furthermore, they demonstrated that there was no spontaneous recovery and that the memory deficit persisted indefinitely. However the goal of this research was to explore cue-dependent amnesia and it was not until Przybyslawski and Sara (1997) conducted a study that current research attempted to replicate cue-dependent amnesia and relate it to existing memory theory. In this experiment, rats learned to navigate a maze to criterion on the first day to demonstrate that the layout of the maze had consolidated. On the second day, they were reexposed to the maze (completed the maze once) as a reminder and afterward were either given the protein inhibitor MK-801 or a placebo. It is known that MK-801 inhibits consolidation and therefore it was hypothesized that rats that were injected with MK-801 would experience a memory deficit as compared to the rats that were injected with the placebo. On day 3, performance on the maze was measured; rats in the protein inhibitor group showed a decrement in performance as compared to rats in the control group. Even more surprising was the persistence of the memory deficit. Researchers found that performance in the MK-801 group revealed a memory deficit even 24 hours later. This study was the first to establish a reconsolidation model showing that reactivating a memory trace triggers cellular events that can be interrupted which results in a deficit in memory performance.

Many other studies of reconsolidation have focused on conditioned fear responses (Eisenberg et al., 2003; Pedreira et al., 2004; Sevenster et al., 2014). Nader, Schafe, and Ledoux (2000) conducted a study that investigated the erasure of fear memory by inhibiting reconsolidation after the presentation of a reminder cue. On day 1, a tone was paired with a foot-shock. Fear responses were measured using freezing, a commonly used indicator of fear in rats. On day 2, rats were given the tone as a reminder of the conditioning but received either the protein inhibitor anisomycin (known to interrupt consolidation of fear memories) or a placebo. Rats that received the inhibitor showed a significant decrease in fear responses on day 3 following the presentation of the tone. Decreases in fear responses were found even when the reminder and inhibitor were administered 14 days after the original learning had taken place. Furthermore, rats that had been given anisomycin, but were not exposed to a reminder tone, showed evidence of a completely intact fear response, providing even more evidence for the reconsolidation hypothesis and showing that even relatively old memories can be altered under the right conditions.

Similar studies have investigated the effects of spatial context. Morris et al. (2006) compared the effects of anisomycin on the reconsolidation of spatial memory in rats under two conditions. In the repeated learning condition, rats were subject to an identical version of the Morris Water Maze so that their performance would reach criterion over the course of 6 days. In the different learning condition, rats were required to encode new spatial information regarding the maze each day leading up to the reactivation phase. The spatial memory that was reactivated in the different learning condition was sensitive to an infusion of anisomycin while reactivation of the single spatial memory which was consolidated over 6 full days (repeated learning condition) was not. In addition to further supporting the reconsolidation hypothesis, the results indicate that the likelihood of reconsolidation depends on the strength of the initial encoding that took place.

It is important to understand the conditions under which the reconsolidation process occurs. In addition to the strength of the memory, prediction error may provide further insight into the boundary conditions of reconsolidation. It is common in reconsolidation research to have a difference between the procedures on day 1 and day 2 (Dudai, 2009; Sevenster, Beckers, & Kindt, 2014). Rescorla and Wagner (1972) presented research showing that prediction error (created by a difference between what subjects expect and by what actually happens) can cause the updating of an existing association; this may be due to a reconsolidation processes. However, it has also been shown that prediction error can cause the formation of a new memory trace rather than updating an existing one, thus establishing one boundary condition on reconsolidation. By the very nature of most reconsolidation paradigms, the learning that takes place on day 2 is not identical to the learning that takes place on day 1. This creates a mismatch between what the subject experiences on day 1 and what they experience on day 2, potentially creating an opportunity to learn something new. Several studies investigated what, if anything, must be inconsistent for reconsolidation to take place. Pedreira, Perez-Cuesta, and Maldonado (2004) examined what would happen if there were no inconsistencies. The crab Chasmagnathus was chosen for a paradigm that used a contextual memory model. In this study, crabs were trained to develop an association between a learning context and a visual danger stimulus. On day 1, crabs were moved from their resting habitat into a spatial learning context that served as a conditioned stimulus. While in the learning context they were presented with a visual danger stimulus (a bright rectangular screen within the cage) which causes freezing. On day 2, crabs were split into two groups; all crabs were again placed into the learning context but one group was again presented with the visual danger stimulus, while the other group was not. The crabs that experienced the visual danger stimulus again were considered to be in the match condition because their experience on day 1 was similar to their experience on day 2. The crabs that were placed into the learning context without the presentation of the visual danger stimulus were considered to be in the mismatch condition. Afterward they were either injected with a saline solution which served as a placebo, or the protein inhibitor cycloheximide. On day 3, crabs were returned to the learning context to measure their fear response in the form of freezing. The results indicated that in the match condition, it did not matter what the crabs were injected with, both groups maintained memory of the conditioning. The crabs in the mismatch condition that were injected with cycloheximide showed a decreased fear response. Crabs that were injected with the placebo still had intact fear memory even in the mismatch condition. Thus, in line with

Rescorla and Wagner's (1972) explanation, it appears that prediction error can induce a need for reconsolidation and an updating of an existing memory.

One factor that may disrupt or modulate reconsolidation is stress. Maroun and Akirav (2007) conducted a study to examine the effects of stress and arousal level on reconsolidation. In this study, stress and arousal were treated as two different variables that were each manipulated independently. Stress is known to impair memory performance (Akirav et al. 2001; Diamond et al. 1996; Lupien and McEwen, 1997; Roozendaal, 2002). RU-486, a glucocorticoid receptor antagonist known to counteract the negative effects of stress on memory consolidation, was used to examine the stress caused by raising rats on an elevated platform. State of arousal was manipulated by exposing half the rats to the learning context several times a day for 4 days before habituating them to the new context. Rats that were habituated in this way had lower levels of arousal during the experiment. On day 1 of the experiment, rats were taken from the home cage and placed into the learning context which was an open field arena with two distinct objects (objects A and B). Twenty-four hours later (on day 2), they were exposed to those two objects again to reactivate the memory trace. Stress was manipulated by placing rats on a brightly lit, elevated platform (known to cause high levels of stress in rats) directly after the reactivation phase. Rats in the low stress group were placed back in the home cage after the reactivation phase. Half the rats that were subject to the elevated platform were also subject to the infusion of RU-486 directly into the basolateral amygdala, while the other half received a saline solution as a placebo. On day 3 (twenty-four hours later), rats were placed into the arena with a familiar and unfamiliar object (objects A and C). Previous research has shown that rats that are presented with both a novel and familiar object will direct more exploration toward the novel object (Ennaceur & Delacour, 1998). The results indicated that rats that were subject to the elevated platform were unable to discriminate object A from object C, suggesting that reconsolidation had been interrupted by the stress. However, RU-486 negated this effect and rats that were subject to both the stressor and RU-486 maintained recognition for object A and showed increased exploration of the novel object C, indicating that the reconsolidation took place. The degree of arousal had no effect on reconsolidation. Stress, in this case, caused a disruption to the reconsolidation process; however, these effects were attenuated in rats that were injected with RU-486.

One concern about reconsolidation is whether it is a necessary concept; that is, is reconsolidation just repeated consolidation? Though some skepticism is to be expected, research provides little evidence that consolidation and reconsolidation share similar underlying processes (Debiec, Ledoux, & Nader, 2002). Instead there is evidence to suggest that consolidation and reconsolidation differ in their molecular requirements and that distinct proteins are required for each (Alberini, 2005; Dudai & Eisenburg, 2004; Debiec et al., 2002). Currently the literature supports the notion that reconsolidation is more than repeated consolidation when it comes to the molecular processes needed for both. However, it is worth noting that the cognitive process may still be very similar.

Research also shows that reconsolidation occurs across different paradigms and species. Fear memory can seemingly be erased by blocking reconsolidation after a reminder of the original fear conditioning is given (Nader et al., 2000). Evidence for reconsolidation as an updating mechanism comes from mismatch paradigms in which researchers create a mismatch between the original learning and the reminder (Pedreira et al., 2004). Stress can also inhibit reconsolidation, showing results that are comparable to pharmaceutical blockades (Maroun & Akirav, 2007).

The animal literature has provided clear evidence supporting the idea that reconsolidation occurs, but it has also shown that it is subject to a number of boundary conditions; for example, reconsolidation is not obligatory for all reactivated memories. These boundary conditions include the importance of the memories that are reactivated by the reminder (e.g., their relevance to survival), the content of new information presented after the reminder (Dudai, 2012), and the strength and age of the original memory. In the animal literature, it is usually the case that the reminder can elicit multiple memory traces. In this case, it has been suggested that the memory that determines behavior is the memory that is reconsolidated (Eisenberg et al. 2003; Pedereira & Maldonado, 2003; Suzuki et al., 2004). It may be possible to select a specific memory trace if an amnesic agent is introduced at a specific time. The kind of new information presented after the reminder is a boundary condition that is still under investigation. Different information presented after the reminder may lead to different results. One important finding regarding this idea has been that new information must be present at the time the reminder is present to trigger reconsolidation (Pedreira, Perez-Cuesta, & Maldonado, 2004). It has also been shown that the interference given after the reminder must be presented within a certain time window after the original memory trace is accessed (Sara, 2000). Despite these restrictions, there is clear evidence of reconsolidation in animals throughout different memory systems including fear, spatial, and episodic memory.

Reconsolidation in Humans

The first evidence of reconsolidation in human participants was in procedural memory (Walker et al., 2003). For example, Stickgold and Walker (2007) conducted a study investigating the effects of sleep on learning and consolidating a finger-tapping task. Participants learned a specific finger-tapping sequence on day 1, slept, and then returned to the lab twenty-four hours later. In one group, participants briefly rehearsed the first sequence before learning a second. In the no rehearsal condition participants learned the second sequence without this reminder. Twenty-four hours later (after they had slept) they returned to the lab for a memory test on both the first and second sequences. Results showed that sleep improved both accuracy and speed for both sequences. However, these effects were reversed if the first sequence was briefly rehearsed on day 2 prior to learning the second sequence. The conclusion was that recalling the first sequence before learning the second brought it back into a labile state and was then susceptible to the interference caused by learning the second sequence.

Reconsolidation has also been used to reduce conditioned fear responses in humans. A study conducted by Kindt, Soeter, and Vervliet (2009) accomplished this by using the beta-blocker propranolol, which has been shown to disrupt reconsolidation in rats after an infusion into the amygdala (Dębiec & LeDoux, 2004). In this study, the conditioned fear response was measured as potentiation of the eye-blink startle response to a loud noise. Participants acquired the appropriate fear response on day 1 and on day 2 received the propranolol or a placebo after memory reactivation (an auditory tone). On day 3, fear response to the original stimulus was measured by eye blink startle response. The results showed that participants who received the propranolol after reactivation had a significantly reduced startle response. This indicates not only that reconsolidation was necessary in order to stabilize the original memory after the reminder, but that we can manipulate the reconsolidation process in order to manipulate the physiological fear response in humans.

It is also possible that a reminder alone is not sufficient to trigger reconsolidation. As noted earlier in the animal literature, it has been hypothesized that reconsolidation is only necessary when there is new information present (Pedreira, Perez-Cuesta, & Maldonado, 2004).

This hypothesis was supported in human fear memory as well (Sevenster, Beckers, & Kindt, 2012). Participants experienced fear conditioning on day 1 by matching pictures of spiders (CS) to an electrical stimulus (US). On day 2, participants were divided into a shock expectancy group and a no-shock expectancy group. All participants received an oral dose of propranolol and memory was reactivated after it was administered. Participants in the shock expectancy group were instructed to remember what they had learned on day 1 (fear conditioning) and shown a single unreinforced CS. Participants in the no-shock expectancy group were also shown a single unreinforced CS but were explicitly told that they would not be shocked. On day 3 all participants were subject to 16 unreinforced CS trials followed by three unsignaled shocks in order to facilitate extinction. Participants were then shown five unreinforced CS trials in order to test the reinstatement of fear. Results indicated that propranolol had no effect on fear responses in the no-shock expectancy group. This suggests that a reactivation of the memory 24 hours later (day 2) did not trigger reconsolidation when the outcome of the CS was perfectly predictable (no-shock). Propranolol only reduced fear responses in the group that expected a shock, but did not receive one. It is important to note that propranolol only reduced fear responses and had no effect on participant's declarative memory of the conditioning. It has since been shown that prediction erroris necessary for the reconsolidation of human associative fear memory (Sevenster, Beckers, & Kindt, 2013). However, prediction error has also been shown to be a boundary condition for reconsolidation as it can cause the formation of a new memory trace rather than an updating of the original learning (Rescorla & Wagner, 1972). Indeed, prediction error that is caused by extinction of the original association can be too dramatic a change for the original memory, causing the creation of a brand new memory trace (Sevenster, Beckers, & Kindt, 2014).

Much of the early research in human reconsolidation focused on procedural and fear memory. However, recent research has started to investigate reconsolidation in human episodic memory. Hupbach, Gomez, Hardt, and Nadel (2007) were among the first to test the reconsolidation hypothesis in human episodic memory as well as the idea that it can be interrupted without the use of pharmaceuticals. In this study participants were asked to memorize a set of objects (balloon, sock, tennis ball, etc.) on the first day. Each item was taken out of a bag, shown to the participant, and then placed into a blue basket. Participants were asked to name each object before it was put away into the basket. Afterward, participants were tested to make sure they had at least 80% accuracy (16 out of 20 items) using free recall. On the second day, reactivation was manipulated by asking a reminder question (can you briefly describe what we did on day 1?). Regardless of whether they received the reminder or not, they learned a new set of items (this time presented without the blue basket in an attempt to make sure that the blue basket itself would not be a reminder). On day 3, two memory tests were given to each participant, this time testing memory for both the day 1 list and day 2 list separately. They found an asymmetrical intrusion pattern for participants in the reminder group: List 2 words were intruded on recall of List 1 more often than List 1 words were intruded on recall of List 2. This result shows that participants were not just making source errors, but that the original List 1 was being updated with new information from List 2. Those in the no-reminder group did not show this effect and overall showed fewer intrusions from either list.

Further research sought to bolster the claim that the asymmetrical intrusion effect reflected reconsolidation and not simply source confusion. Hupbach, Gomez, and Nadel (2009) conducted a study that addressed this specific question. The procedure up to day 3 was identical to the previous study. However, the test protocol on day 3 included a single recognition test over both lists and a source attribution task. During testing on day 3, participants were presented with items from List 1 and List 2 one at a time and asked if the item was old (studied), or new. If the item was considered old, participants were then asked to decide whether the object was presented on day 1 or day 2 and a confidence judgment was made on a scale from 1 to 5 with 1 being “not sure” and 5 being “absolutely sure”. Results again showed the asymmetrical intrusion effect for subjects who received a reminder on day 2. These results supported the conclusion that reconsolidation for episodic memory causes an updating of the original memory, not just source confusion.

Though some reminders in human reconsolidation research are explicit (a verbal question asking about the original learning), others have been much subtler. In another study, a paradigm similar to Hupbach’s research was used, but the stimuli were pairings of nonsense syllables presented on a computer screen rather than physical objects (Forcato, Burgos, Argibay, Molina, Pedreira and Maldonado, 2007). Participants were instructed to memorize the pairings. The participants in the reminder group were shown a single cue from List 1 before learning the second List on day 2. After the cue was shown and before subjects could type in the target, a notice appeared on the screen which announced that the session had to be suspended. Despite the difference between the reminders, the results were similar to the results of Hupbach et al. (2009) in that participants showed an asymmetrical intrusion effect when the memory of List 1 was reactivated by a reminder. These results also showed that reconsolidation applies not just to objects, but to lists of words as well.

Similar to findings in the animal literature, studies in the human literature have shown that prediction error may be necessary for reconsolidation. Forcato, Argibay, Pedreira and Maldonado (2009) further investigated the relevance of the reminder structure. Participants were instructed to memorize a list of cue-target pairs on day 1. On day 2, participants were divided into 3 conditions which varied the nature of the reminder that was given before a fabricated computer error (similar to the procedure from the previous experiment) terminated the reminder portion of the experiment before learning List 2. The context-reminder group returned to the room used for day 1 before the computer crash and moving on to learn List 2. The cue-reminder group experienced the same context and was presented with one cue from List 1; however, the computer "crashed" before they had a chance to remember the target and they moved on to learning List 2. The response-reminder group experienced the context from the first day and was allowed to respond to the cue before the computer "crashed". On day 3, each participants' memory for List 1 and List 2 was tested using cued recall. The results indicated that only the cue-reminder group showed the asymmetrical intrusion effect. The conclusion was that reconsolidation was only triggered when expectations were violated due to the fake computer error (i.e., participants couldn't respond to the cue). This finding is similar to an important finding in the animal literature which showed that reconsolidation was not necessary when there was no new information to be learned during the reminder (Pedreira et al. 2004). In this case the response group was able to complete a full trial from the study phase before the fabricated computer error occurred. This is thought to have negated the need for reconsolidation.

Not all reminders are successful in triggering reconsolidation. A recent study manipulated different kinds of reminders and concluded that spatial context was the most important (Hupbach et al., 2008). Three conditions, each with a different reminder, were used in this study. In the spatial context condition, spatial context served as the reminder and was simply held constant for List 1 and List 2 while the other variables (such as the experimenter), were different. In the experimenter condition, the experimenter was the reminder; thus, day 2 took place in a different room than day 1, but the experimenter remained the same. Finally, in the question condition, participants learned List 2 in a different room and with a different experimenter but were asked the question "Can you briefly describe the procedure from day 1?" Intrusions from List 2 were found in all conditions, but a one-way ANOVA revealed they were only significant in the spatial context condition. In this case, being in the same room in the spatial context condition was a reminder which triggered reconsolidation, however the reminders in the experimenter and question conditions did not trigger reconsolidation and in these conditions memory for List 1 was left relatively intact. It is possible that space is the most important aspect of a good reminder because other parts of a reminder (such as the experimenter in this example) are built on top of the spatial context that they were presented in, such that changing spatial context would remove the foundation for other parts of the memory. If this is the case, then these results make sense because changing the spatial context would, in effect, remove the scaffolding underlying both events. However, spatial context alone appears to be enough to trigger reconsolidation. Another explanation could be that these changes were too big, and like the findings in associative fear memory (Pedreira, Perez-Cuesta, & Maldonado, 2004), a new memory trace was created rather than an updating of the original. However, these results still leave some questions unanswered. For example, in this experiment there was no control group, so every group received a reminder. The fact that spatial context was the only successful reminder conflicts with other research (Forcato et al., 2009). Importantly, Forcato et al. did not find evidence of reconsolidation despite using the same spatial context, suggesting that spatial context may not always be necessary.

It is difficult to explain with certainty why spatial context is not always an effective reminder. Another study investigating spatial reminders found that environmental context was an effective reminder but only when the context was unfamiliar (Hupbach, Gomez, & Nadel, 2011).

In this study 5-year old children were tested. In their first experiment, participants learned a set of objects on day 1 in an unfamiliar room at their daycare. On day 2 they learned a second set of objects either in the original room (so that spatial context was the only reminder), or a different room that was also unfamiliar. Results replicated previous findings and children who learned set 1 and set 2 in the same spatial context showed a significant number of intrusions from List 2 into List 1. In their second experiment, participants underwent a similar procedure but learned both sets in their own homes. In contrast to experiment 1, half of the participants were asked a reminder question about day 1 before learning the new set on day 2 as well as having the same experimenter present on both days. These variables were both shown to be insufficient reconsolidation triggers in previous research when environmental context was unfamiliar (Hupbach et al., 2008). Children who were tested in their own homes and did not receive any other reminders (experimenter or question) did not produce a significant number of intrusions while children who were accompanied by the same experimenter and asked a reminder question, did.. Thus, the results of experiment 2 indicated that spatial context is only an effective reminder when it is unfamiliar.

Overall, there is a lot of support for the fact that reconsolidation occurs in humans. Early human research that focused on fear memory has shown that it is possible to eliminate the physiological response to fear through the blockade of reconsolidation. Other research has shown that blocking reconsolidation with the use of propranolol could one day be useful in the treatment of post-traumatic stress disorder (Brunet, Orr, Tremblay, Robertson, Nader, & Pitman, 2008). Further, fear memory research has shown that prediction error is necessary for the reconsolidation process to occur. Overall, while the evidence of reconsolidation in humans often parallels those found in non-human animals, the specific boundary conditions for episodic memory are still debated (e.g., the exact role of spatial context).

CHAPTER 3

THE CURRENT STUDY

Reconsolidation has received a lot of attention by researchers in the last decade but there are still many questions left unanswered. Through reconsolidation it may be possible to strengthen or weaken a memory after reactivating that specific memory trace and returning it to a labile state. Reconsolidation has been shown in different species and in different memory systems. Previous research suggests that space may be a particularly important factor to trigger reconsolidation. The goal of the study was to gain insight into how and why reconsolidation is triggered.

The discrepancy in the results between Forcato's and Hupbach's work leaves the unanswered question, is space necessary even if there are other salient reminders? For Experiment 1, I manipulated spatial context as well as the presence of an external salient reminder that is not linked to spatial context. The goal of Experiment 1 was to investigate the role of spatial context versus other reminders in triggering reconsolidation. Hupbach's studies, which used spatial context in conjunction with other forms of a reminder, suggest that spatial context is the most effective reminder (and possibly the only one that matters when it is unfamiliar) when it comes to triggering reconsolidation, while Forcato's research showed that spatial context may not be able to trigger reconsolidation unless expectations are violated. The importance of spatial context is also brought into question when we consider the animal studies that required reminders other than spatial context to see reconsolidation effects (Pedreira et al., 2004). In Experiment 1, I tested the idea that spatial context is key to triggering reconsolidation by including another very salient piece of information as a reminder (a brightly colored pink laptop sleeve). Unlike Hupbach's studies, the external reminder was present throughout the experiment and therefore could serve as the new “scaffolding” for each memory. If all other information is associated with spatial context like Hupbach and colleagues’ work suggests, then the external reminder should lose its effectiveness and not be able to trigger reconsolidation when it is seen in a different spatial context. Spatial context was manipulated by having participants return to the lab, or a different building location on day 2. The external reminder (the pink laptop sleeve) was either present or absent for the duration of the study. When it was present, participants may have seen the external reminder in a similar way to how spatial context was used in Hupbach’s experiments. In those experiments, external reminders were fundamentally different from space because they were not present throughout the duration of the experiment. These two factors were crossed, creating a 2x2 design. It was expected that the reminder group, even in a different spatial context, would show an asymmetrical intrusion effect comparable to the no-reminder group that was in identical spatial context but did not have an external reminder. More importantly was expected that the group that recieved no reminder and was not in the identical spatial context on day 2 would not experience any reconsolidation effects and would not show a significant asymmetrical intrusion effect (see Figure 2).

The goal of Experiment 2 was to investigate what constitutes a mismatch or a violation of expectations; that is, what kind of mismatch will trigger reconsolidation? Is a different physical experience between day 1 and day 2 necessary to trigger reconsolidation? Do simple conscious expectancies matter? The variables were the participants’ expectations of what would happen on day 2 and what would actually happen on day 2. Participants went through a unique procedure on day 1 (shooting a Nerf basketball through a hoop) before learning List 1. Because I manipulated expectations in Experiment 2, it was important that participants have a definite idea of what they were to expect on day 2. Before they left, participants were told that they would be doing either the same thing on day 2 or something different. When they returned on day 2, participants were assigned to a condition in which their expectation is either matched (e.g., completing the basketball task again when they were expecting to) or is violated (e.g., completing a new task when they expected to repeat the procedure from day one). It was expected that participants who had their expectations violated would have a greater asymmetrical intrusion effect when memory was tested on day 3. This would suggest that reconsolidation is an updating procedure and might only be necessary when participants' expectations are violated, regardless of the reality of the situation.

Experiment 1

The purpose of Experiment 1 was to investigate the role of spatial context in triggering reconsolidation. This was tested using a 2x2 design in which the between subjects variables were spatial context (same or different) and the presence of an external reminder (bright pink laptop sleeve will either be present or absent).

Method

Participants

Participants included healthy adults (ages 18-42, *M* = 19, *SD* = 5) recruited from the University of Nevada, Las Vegas subject pool. A total of 72 subjects (17 male, 55 female) participated in Experiment 1; 18 participants were randomly assigned to each condition. Participants recruited through the subject pool were compensated with partial course credit. Participants were randomly assigned to a same or different context group as well as a reminder or no-reminder group.

Materials

Fifty words from the MRC psycholinguistic database were used. Words were split equally into 2 lists. List 1 and List 2 consisted of 25 unrelated words each. Words were of middle to high frequency (List 1 *M* = 103; List 2 *M* = 102) and between 4 and 5 letters each (List 1 *M* = 4.76; List 2 *M* = 4.88). Lists were counterbalanced such that each list appeared equally often as List 1 and List 2. The order in which participants were asked to recall the lists was also counterbalanced. A laptop was used to administer the materials regardless of location. The laptop was in a hot pink laptop sleeve in the external reminder conditions. The sleeve was present during the duration of the sessions. A questionnaire was given at the end of day 3.

Procedure

Participants came into the lab for three sessions that took place on three consecutive days. Participants were informed that they would be learning different lists and asked to recall them later. Participants were run individually. All participants signed an informed consent sheet before taking part in the experiment.

On day 1, participants studied words from List 1 that were shown one at a time on the laptop screen for 4000 ms. The bright pink laptop sleeve was visible throughout the procedure on day 1. Afterwards, participants were asked to recall the words from List 1[1]. If fewer than 20 words (80%) were recalled, participants repeated the learning process and were tested again. Similar to Hupbach et al, 2007, once five learning trials took place, or at least 20 words were recalled, the session ended. If participants were unable to reach criterion after five learning trials, they were excluded from the analyses, and informed that the experiment had concluded.

On day 2, participants were split into the four experimental groups. Spatial context was manipulated by administering List 2 either in the same lab setting, or in a study area of the Lied

[1] Participants typed in the words and were able to see their responses. The backspace key could be used to correct a misspelling but once a word was entered it could not be changed.

Library at the University of Nevada, Las Vegas. The external reminder was either present (the bright pink laptop sleeve was placed next to the laptop) or absent. These conditions were crossed, forming a 2x2 design. List 2 presentation was identical to the presentation of List 1 for all groups.

On day 3, the experimenter led participants into the lab and were asked to recall the words from both lists, one list at a time. Recall was self-paced and participants were asked to recall all 25 words. They were instructed to guess as needed to fill in any remaining blanks. A questionnaire was given after the test on day 3 to assess if any specific memory strategies were used, and also to determine if the bright pink laptop sleeve was salient and memorable.

Results

Acquisition Performance

The number of blocks that were required for each participant to recall at least 20 words was recorded. On day 1, participants took an average of 2.91 learning trials to reach criteria (SD = .86). On day 2, participants took an average 2.47 learning trials to reach criteria (SD = .74). There were no differences between any of the groups for either day. A two-way analysis of variance (context by cue) was conducted to compare the number of trials between lists across all conditions. There were no significant effects (all *F*'s < 1).

Free Recall

A 2x2 ANOVA (context by cue) that was used to analyze *day-3* recall performance for List 1 and List 2 did not reveal any differences between conditions, List 1: $F_{(3, 71)} = 0.73$, $p = .534$; List 2: $F_{(3, 71)} = 0.32$, $p = .800$. However overall differences in accuracy between the lists was significant $t_{(71)} = -4.97$, $p < .001$. List 1 $M = 12.51$, List 2 $M = 15.22$, with higher recall for Day 2.

Asymmetrical intrusion effect.

I used a difference score to calculate the asymmetrical intrusion effect. It is the number of intrusions from List 2 into List 1 minus the number of intrusions from List 1 into List 2 for each participant. A positive number shows that more intrusions were made from List 2 into List 1, indicating that reconsolidation has taken place. The asymmetrical intrusion effect was analyzed using a two-way ANOVA (See Figure 2). Results of this analysis indicated that participants had a lower asymmetrical intrusion score when an external reminder was present ($F_{(1, 72)} = 5.11$, $p = 0.027$), and when they returned to the same spatial context ($F_{(1, 72)} = 10.32$, $p = 0.002$). The interaction term was not significant ($F_{(1, 72)} = 1.51$, $p = .223$).

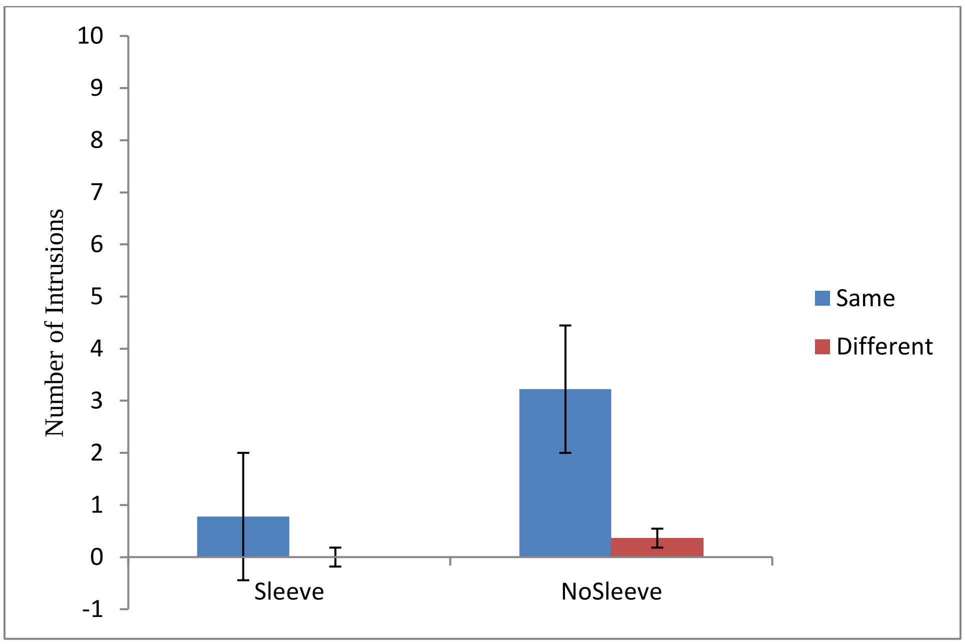


***Figure 2*. Asymetrical Intrusion Effect**

Intrusions specific to each List

In order to make sure that this outcome was not just the result of this difference score, we conducted a similar analysis looking at each list's specific intrusions. Previous research has not used a difference score and typically only reports intrusions from List 2 into List 1. The analysis for each list is kept separate in order to highlight the effects of one-way intrusions as well as diminish the importance of the small number of intrusions from List 1 into List 2. The intrusions from List 2 were analyzed using a two-way ANOVA. The analysis revealed a main effect of both the presence of an external reminder ($F_{(1, 72)}$ = 4.45, p = 0.038, η^2 = .062), as well as spatial context ($F_{(1, 72)}$ = 9.78, p = 0.003, η^2 = .162). The interaction was not significant ($F_{(1, 72)}$ = 3.82, p = .055). Counter to the original hypothesis, post hoc comparisons revealed that participants who had an external reminder made fewer intrusions. However, participants who returned to the same spatial context on day 2 made a greater number of intrusions than those who were in a different spatial context. Intrusions into List 2 were analyzed using a two-way ANOVA. The ANOVA showed no significant effects of external reminder ($F_{(1, 72)}$ = .025, p = 0.874), or spatial context ($F_{(1,72)}$ = 0.014, p = 0.958). The interaction term was non-significant ($F_{(1,72)}$ = 1.02, p = 0.316).

Discussion

The presence of a reminder did not affect memory performance for either list, however it appears that similar spatial context did serve as a sufficient reminder of the original learning, triggering memory updating. When asked to recall List 1, participants who studied List 2 in the same context (the lab) were more likely to intrude words from List 2 than participants in the different context conditions. These results replicate findings from previous studies (Hupbach, et al., 2008; Hupbach, Gomez, & Nadel, 2011) that demonstrated that learning new information in the same spatial context can contribute to a need for memory updating. Interestingly, the presence of an external reminder had the opposite effect. In contrast to our hypothesis, the presence of an external reminder may have led participants to make fewer intrusions into List 1. Reasons for this are still unclear. However, there were three outliers in the no-cue condition that likely contributed to a higher mean for their group which could be driving this effect. A Dixon's

Q test outlier analysis did not reveal any of the outliers to be significant, though this is likely due to a small sample size.

It is important to note that the majority of previous research on reconsolidation employed a different procedure during the final recall task. In most studies participants recalled either list 1or list 2 in the final session, but in this study participants recalled both lists. While this within-subjects design allowed for more conservative conclusions, it also introduced a potential problem. The data revealed that participants often copied words from one list to another during final recall tasks, despite specific instructions not to do so. This copying problem makes it difficult to draw conclusions about intrusions because of the order of the tests. However, a separate analysis was conducted using only data from participants who had their memory for List 1 test first. This analysis mimicked the overall AIE analysis, showing a significant main effect of spatial context, $F_{(3, 37)} = 6.72$, $p = 0.014$, but not for external reminder, $F_{(3, 37)} = .296$, $p = 0.590$. In addition, a separate ANCOVA for the asymmetrical intrusion effect was conducted, using the number of copies as a covariate. Results of this analysis mimicked the previous ANOVA in both direction and significance, showing a main effect of external reminder, $F_{(1, 72)} = 4.30$, $p = 0.042$ and spatial context, $F_{(1, 72)} = 11.18$, $p = 0.001$. However, it is still unclear to what extent these copies affected the results of this study, as it is difficult to ascertain whether a word is an intrusion by memory or just a copy because it was recalled on a previous list. The instructions were clarified in the next experiment to address this.

Experiment 2

The purpose of Experiment 2 was to investigate the effect of expectations on reconsolidation. This was tested using a 2x2 design in which the between subjects variables were the expectation of a specific procedure and the physical procedure itself (see Table 1). I anticipated evidence of reconsolidation when participant's expectations were violated, regardless of the reality of the situation.

Table 1

Is Reconsolidation Necessary?

	REALITY SAME	REALITY DIFFERENT
EXPECT SAME	This is a MATCH Reconsolidation should NOT be needed.	This is a NON-MATCH Reconsolidation SHOULD be needed.
EXPECT DIFFERENT	This is a NON-MATCH Reconsolidation SHOULD be needed.	This is a MATCH Reconsolidation should NOT be needed.

Method

Participants

Participants included healthy adults (ages 18-43, $M = 19$, $SD = 3$) recruited from the University of Nevada, Las Vegas subject pool. A total of 72 subjects (34 males, 38 females) participated in Experiment 2; 18 participants were randomly assigned to each condition. Participants recruited through the subject pool were compensated with partial course credit. Participants were randomly assigned to the four conditions.

Materials

The materials and counterbalancing were the same as that used in Experiment 1. A Nerf basketball set consisting of an orange foam ball and a plastic net hung over a door frame was used, along with a list of 6 YouTube videos consisting of cats and other small animals between

15 and 30 seconds long were used to create two distinct procedures. A questionnaire was given at the end of day 3.

Procedure

Participants came into the lab for three sessions that took place over three consecutive days. Participants were informed that this was a learning experiment. Participants took part in the study individually. All participants signed an informed consent form before taking part in the experiment.

On day 1, all participants arrived in the lab and were informed that this study investigates different types of learning in order to justify novel procedures. They completed a Nerf basketball task which consisted of participants attempting to score as many baskets as possible, standing approximately 10 feet away, within a two-minute time period. Scores were recorded. After the basketball task, participants began encoding the first list, which they were told to remember. Words were presented one at a time and each word remained on screen for 4000 ms. After the study phase, participants were asked to recall as many words as they could. Similar to Experiment 1, if fewer than 20 words (80%) were recalled correctly, participants repeated both study and test; this persisted until at least 20 words were recalled or they reached a maximum of five learning trials. In contrast to experiment 1, participants who were unable to reach criterion were not excluded from the study. To manipulate expectations, participants in the *expect-same* group were told that they would be repeating the Nerf task when they returned on day 2. Those in the *expectation-different* group were told that they would be rating the entertainment value of YouTube videos instead of completing the Nerf basketball task on the second day (See Table 1).

On day 2, participants in the *expectations-met* group completed the task they were told they would do. Participants in the *expectations-violated* group completed a different task than the one they were told they would be completing. Participants who were in the video rating task rated a series of YouTube videos on how entertaining they were. Ratings were recorded on a scale from 1 to 5, 5 being the most entertaining. All the videos together totaled a length of about two minutes. The presentation of List 2 was the same as day 1 and took place after completion of the chosen task. Participants were asked to recall the words from only List 2 after presentation of List 2 and were required to meet the criterion.

On day 3 participants recalled words from both lists, one list at a time. In order to address the copying problem described in Experiment 1, the researcher instructed participants that each word was only to be used once and could not be submitted for both lists. Participants were asked to recall all 25 words and to guess as needed in order to fill in any remaining blanks. Participants were asked to first write down all the words they remembered before writing "1234" in one of the blanks to indicate that they had started guessing. The order in which participants were asked to recall the lists was counterbalanced and responses were not timed in any way. After the recall phase, a questionnaire about each participant's experience in the study was given as a manipulation check to make sure expectations were violated if the condition called for it. For example, I asked participants to note if the researcher had been mistaken about the procedure they would complete on day 2.

Results

Acquisition Performance

The number of blocks that were required for each participant to recall at least 20 words was recorded. On day 1, participants took an average of 2.70 (*SD* = 0.84) learning trials to reach criteria. On day 2, participants took an average 2.57 (*SD* = 1.02) learning trials to reach criteria. There were no differences between any of the groups for either day. A two-way analysis of variance (expectation by reality) was conducted to compare the number of trials between lists. There were no significant effects (all *F*'s > 1).

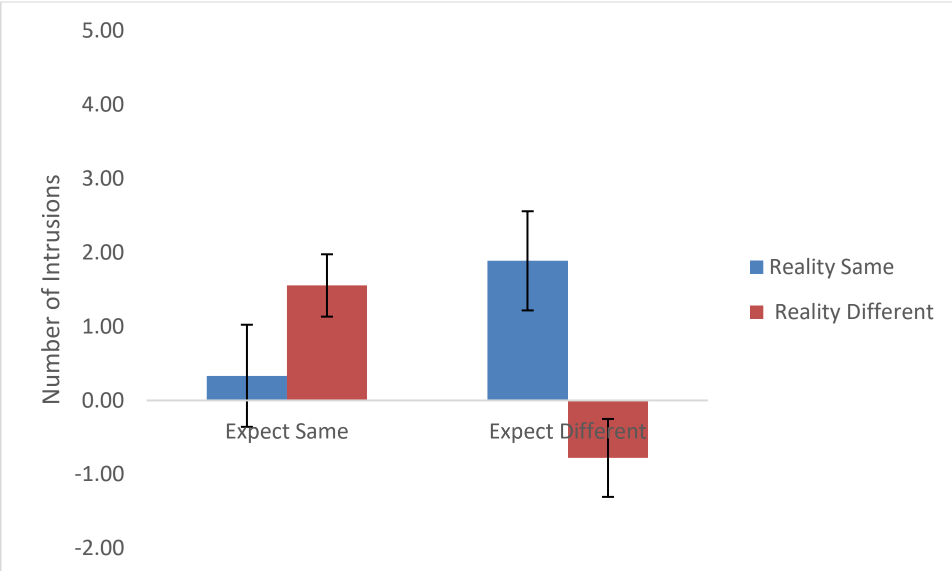
Free Recall

Day-3 recall performance for List 1 and for List 2 did not differ as a function of group (List 1: $F_{(3, 71)} = 0.53$, $p = .659$; List 2: $F_{(3, 71)} = 1.49$, $p = .223$). Differences in accuracy between the lists was non-significant $t_{(71)} = -0.79$, $p = .431$. List 1 $M = 11.90$, $SD = 5.52$; List 2 $M = 12.59$, $SD = 5.23$.

Asymmetrical intrusion effect.

Means for the asymmetrical intrusion effect are presented in Figure 3. The asymmetrical intrusion effect was calculated the same way as in experiment 1 and was analyzed using a two-way ANOVA with expectations (met vs. violated; between subjects) and the reality (same vs. different; between subjects). Results of this analysis indicated that participants had a higher asymmetrical intrusion score when their expectations were violated ($F_{(1, 72)} = 10.93$, $p = .002$, $\eta^2 = .138$). The effect of reality (whether or not they repeated the same procedure) was not significant ($F_{(1, 72)} = 1.50$, $p = .224$) The interaction term was also not significant ($F_{(1, 72)} = 0.43$, $p = .511$).

Figure 3 Asymmetrical Intrusion Effect



List Specific Intrusions

The number of words that were from List 2, recalled during List 1, was analyzed using a two-way ANOVA. The analysis revealed a marginal effect of expectation ($F_{(1, 72)}$ = 3.45, p = 0.068, η^2 = .048). There was no main effect of reality ($F_{(1, 72)}$ = 0.78, p =.378). The interaction was not significant ($F_{(1, 72)}$ = 0.007, p =.936). The analysis suggests that a violation of expectations led to more intrusions from List 2, regardless of whether participants repeated the same procedure. Intrusions from List 1 into List 2 were analyzed using a two-way ANOVA. The ANOVA showed no significant effects of expectation ($F_{(1, 72)}$ = 1.72, p = 0.193), or reality ($F_{(1,72)}$ = 0.048, p = 0.827). The interaction term was not significant ($F_{(1,72)}$ = 0.76, p = 0.384).

Discussion

There were no differences in recall scores between List 1 and List 2 during day-3 recall. Participant expectations, as well as the procedures for each day, had no effect on recall scores for List 1 or List 2. However, it appears that violating participant expectations did trigger memory updating, supporting my hypothesis that participants who were misled about the procedure for the following day would produce higher asymmetrical intrusion scores. Importantly, the actual day 2 procedure did not have an effect on their asymmetrical intrusion score, showing that the effect of violating expectations was not just a product of participants undergoing a different procedure from day 1. These results are consistent with Forcato et al. (2007), who demonstrated that reconsolidation was only necessary when expectations were violated through the use of premature termination of the procedure. The present experiment sought to extend this idea to conscious expectations and show that reconsolidation may only be necessary when memory updating is triggered through a violation of those expectations.

Participants were able to indicate whether their conscious expectations were violated through the post experiment questionnaire. Participants responded with either a yes or a no when asked if the researcher had been mistaken about the procedure they should expect on day 2. Those who responded ‘no’ may still have had violated expectations (due to the wording of the question), the effect of expectations was still robust when those individuals were removed from the analysis $F_{(1, 66)} = 12.78$, p =.001, $\eta^2 = .171$.

It is worth noting that unlike experiment 1, experiment 2 did not show significant effects when only looking at individual list intrusions and only showed a main effect of expectations in the asymmetrical intrusion analysis. However, the results for List 2 intrusions into List 1 were approaching significance (p = .068) and I believe it is likely due to low sample size. None of the manipulations for experiments 1 or 2 had any effect on List 1 intrusions into List 2, providing support for the reconsolidation hypothesis.

CHAPTER 4 GENERAL DISCUSSION

In contrast to the animal literature, reconsolidation research in humans has produced few theories for the boundary conditions of the reconsolidation process. Some even argue that reconsolidation in humans does not merit further research as it can be explained through the misinformation effect. Indeed, there are many similarities between the two paradigms, and while the evidence that reconsolidation does exist in humans is growing, only a portion of new research aims to cement its existence within the human episodic memory system. In order to try and further the human reconsolidation literature, the current study aimed to further illustrate some of the boundary conditions of the effect and although both of the above experiments provide evidence for the reconsolidation hypothesis within the human episodic memory system, it is clear that the field has a long way to go before the exact boundary conditions are understood.

Experiment 1 demonstrated that reconsolidation occurs when learning and new learning take place within the same spatial context, replicating the results of Hupbach et al. (2007). Experiment 2 provided evidence for the hypothesis that reconsolidation occurs when new learning takes place after a violation of expectations. Previous research on reconsolidation within the human episodic memory system has suggested that it is only spatial context that determines whether or not reconsolidation takes place (Hupbach et al., 2007; Hupbach, Gomez, Nadel, 2011). Though experiment 1 and experiment 2 replicated Hupbach's and Forcato's results respectively, I also replicated the inconsistencies between the two lines of research regarding the importance and effectiveness of spatial context. While it seems that an external reminder (unlike spatial context) is not sufficient to trigger reconsolidation (Experiment 1), experiment 2 showed that similar spatial context does not always trigger reconsolidation. In experiment 2, I showed evidence of reconsolidation when expectations were violated. Importantly, it seems like reconsolidation did not occur within conditions in which expectations were met, even though the entire experiment took place within the same spatial context. The future of reconsolidation research may be in identifying what makes spatial context so influential in some studies (Hupbach et al., 2007; Hupbach, Gomez, Nadel, 2011), but irrelevant in others (Forcato et al., 2007). So far it appears that spatial context plays a key role in reconsolidation, but only when spatial context is observed or manipulated. It is entirely possible that spatial context somehow allows for reconsolidation to take place but does not necessarily cause the process to occur. Perhaps we can turn to the rat literature for an answer. Many studies that observe a reconsolidation effect in rats return the subjects to the same spatial context after the administration of the drug (Przybyslawski & Sara, 1997; Dudai & Eisenberg, 2004; Dudai, 2009). It is possible that returning rats to the same spatial context allows the reconsolidation process to occur but does not necessarily trigger it.

Given the inconsistencies among the effects of spatial context, it is important to note a large difference in the day 3 procedure between the current study, and that of previous research (Hupbach et al., 2007; Hupbach, Hardt, Gomez, & Nadel, 2008). While Hupbach typically treats List recall on day 3 as a between subjects variable, asking participants to only recall either List 1 or List 2, the current study treated List recall on day 3 as a within subjects variable, asking participants to recall both lists, one right after the other. Though this is what lead to a potential problem in the results of the current study (discussed below), it is also what allowed stronger claims to be made about the direction of the list intrusions. More specifically, this allowed for the use of a difference score, the asymmetrical intrusion effect as the primary dependent variable. This is also in contrast with Hupbach's studies, as only intrusions from List 2 into List 1 are reported in those studies.

Because of this difference, a potential extraneous variable was found during the analysis. As such, it is important to use caution when interpreting the results from experiment 1. Some participants appeared to simply copy the words they recalled on the first list tested on day 3 onto the second list tested. In an attempt to lessen the effect of these copies, the number of words that were the same on both test lists was used as a covariate in an analysis of covariance. Even though this ANCOVA yielded similar results to the original analysis, it is impossible to determine exactly to what extent this copying problem affected the results. However, a separate analysis was run, using only data from participants who were asked to recall List 1 first so that only words that were not copies found their way into the analysis. Though this cut the already small sample size in half, the results were again consistent with the original ANOVA.

It is clear that the exact boundary conditions to reconsolidation are still ambiguous and further study is required in order to fully understand the process. Moving forward, it may be important to address some of the other theoretical concerns with the reconsolidation paradigm. One of the more intriguing questions to be answered has to do with the timeframe that almost all reconsolidation studies use. Is it possible to trigger a reconsolidation process within a feew hours rather than a few days? What moderates the importance of spatial context? Could reinstating spatial context through mental imagery be enough to trigger reconsolidation? Does reconsolidation still occur when violation of expectation takes place in a difference spatial context? What if different spatial context is what causes the expectation to be violated? These are just a few of the questions that should be addressed moving forward.

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CURRICULUM VITAE

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Educational History

2013 – Current University of Nevada, Las Vegas M.S. Spring 2015 (Expected)
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2008 – 2012 University of South Florida B.S. Fall 2012
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Psychology Honors Program, Major GPA 3.67
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Professional Memberships

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Research Experience

August 2013- present Graduate Assistant, Human Memory Lab

- **Supervisor: Colleen Parks, Ph.D.**
- I work in the lab, running participants and collecting data.
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January 2012 – May 2013 Senior Research Assistant, Cognitive Psychophysiology Lab

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- I volunteered in research about subsequent memory patterns involving the P300. I apply EEG nets on participants and used the programs E-Prime and NetStation.
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- I volunteered on a study about participants' willingness to cheat.
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Publications

Conference Presentations

Kiley, C., Kamp, S., Donchin, E. **The P300 Subsequent Memory Effect Elicited by the First Word in the List Depends on its Output Position During Recall**. *Annual meeting of the Cognitive Neuroscience Society, San-Fransisco, CA, USA, 2013*

Kiley, C., Parks, C. **Reconsolidation: The Effects of Spatial Context and Expectations.** *University of Nevada, Las Vegas Research Forum, NV, USA, 2016*

Teaching Experience

Lecturer	Cognition	Fall 2014	University of Nevada, Las Vegas
Instructor	Psychology 101	Fall 2015	University of Nevada, Las Vegas
Instructor	Psychology101	Spring 2016	University of Nevada, Las Vegas