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Reconsolidation: Unique Cognitive Process or State Dependent Learning?

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RECONSOLIDATION: UNIQUE COGNITIVE PROCESS OR STATE DEPENDENT LEARNING?

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Abstract

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 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. However, it is still unclear when the effect will occur. Some studies suggest that reconsolidation is only necessary when new information is presented in the same spatial context or when prediction error occurs. More recent work has provided evidence that reconsolidation could be due to state dependent learning. Here, we aim to determine if an existing cognitive phenomenon, such as state dependent learning, can explain various reconsolidation effects. Experiment 1 examined that possibility using mood as internal states and then matching or mismatching moods during select study days and test. Experiment 2 further expanded on this possibility by matching (or mismatching) states on all days throughout the experiment.

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Introduction

The reconsolidation hypothesis suggests that retrieval of an existing memory trace can destabilize it. This in turn opens a time dependent window during which the memory trace is malleable. The memory in question can then be altered, strengthened, or weakened (Inda, Muravieva, & Alberini, 2011; Sara, 2000). Support for this theory is largely drawn from nonhuman animal studies that use invasive pharmacological interventions to disrupt the post-retrieval reconsolidation process. In comparison to the animal literature, reconsolidation in humans has less evidence to support its existence, especially in the episodic memory system (Alberini & LeDoux, 2013). These human episodic studies often claim that post retrieval learning can be used as an update process that can change existing memory traces (Hupbach, Gomez, & Nadel, 2009). This idea warrants scrutiny due to the incredible number of theoretical and clinical applications, including treatment of various phobias and post-traumatic stress disorder (Debiec & Ledoux, 2006). While reconsolidation is a fascinating theory, the question remains whether it is a newly discovered process or is something that can be explained using previously established concepts such as a temporal model of memory (Sederberg et al., 2011), the existing consolidation theory (Alvarez & Squire, 1994; Nader, Schafe, & LeDoux, 2000), or state dependent learning (Tulving & Thomson, 1973).

The first study to demonstrate reconsolidation effects was Misanin, Miller, and Lewis (1968). In this study rats showed a reduction in fear memory when a brief reminder of the original learning was presented and followed by an electroconvulsive shock (ECS), a treatment known to cause amnestic effects when applied in the early stages of consolidation. The effect from this experiment was termed “cue-dependent amnesia” and this paradigm has served as the basis for many reconsolidation studies see Figure 1). The research that followed was dedicated to replicating and exploring this phenomenon. Bregman, Nicholas, and Lewis (1976) found that if rats were given an electroconvulsive shock at the start of a previously consolidated maze, they would experience an amnesic effect and would no longer be able complete the maze without errors. Furthermore, their memory for the maze remained impaired days after the initial shock. The goal of this research was to explore cue-dependent amnesia and it was not until Przybyslawski and Sara (1997) that research began to delve into this phenomenon and relate it to existing memory theory. In their experiment, rats learned to navigate a maze on the first day and would learn it to criterion to demonstrate that the memory of the maze layout had consolidated. On the second day, they were re-exposed to the maze by running through it once as a reminder. After reactivation of the maze, they were either given a protein synthesis inhibitor or a placebo. It has been established that protein synthesis inhibitors have a detrimental effect on memory consolidation and therefore it was hypothesized that rats injected with one after activating the memory of the maze, would experience a memory deficit as compared to the rats that were injected with the placebo. Like most reconsolidation experiments today, Day 3 was a test day and the rat's performance on the maze was measures. Rats in the protein inhibitor group showed a decrement in performance as compared to rats in the control group. Researchers also found that performance in the protein inhibitor group was impaired even 24 hours later, replicating the length of the memory deficit from previous studies. This study was also 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.

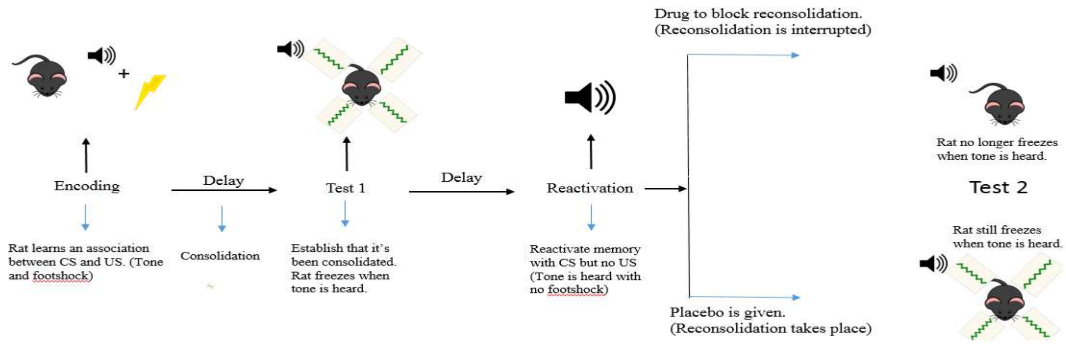

Figure 1: Typical 3-day reconsolidation paradigm in animal literature

The 3-day paradigm used in the aforementioned studies has become very common within the current reconsolidation literature. Though the times between sessions (or days) sometimes vary, both human and animal studies alike make use of this design to test potential reconsolidation effects. During session 1, the subjects in a reconsolidation study are exposed to an initial learning event. Information introduced during session 1 is typically learned to criterion. This is to ensure that an established memory trace can be manipulated in some way during session 2. The second session typically takes places between 24 and 48 hours later, and in some conditions, a reminder is given to activate the memory trace from session 1. In a majority of the human literature, it is during session 2 where most of the experimental manipulation takes place. This is where a lot of the differences lie between reconsolidation studies, especially when considering the human and animal domains. In many human studies, additional information is introduced during session 2. This new information is hypothesized to update the original learning, so long as the original learning requires reconsolidation. The end result is typically an integration of the new information into the original learning (Schiller et al., 2010). Though session 2 differs significantly between studies, session 3 is a test session. In human studies, researchers look to see how much new information (session 2) has intruded into the memory trace for session 1. In animal studies, researchers compare retention levels for subjects that received a protein synthesis inhibitor with those that did not.

Though procedural and fear memory make up a large percentage of studies investigating reconsolidation (especially in much of the older literature), more recent work has delved the effects that reconsolidation has on human episodic memory. Hupbach, Gomez, Hardt, and Nadel (2007) established that not only could reconsolidation effects be found in the human episodic memory domain, but that they could be elicited without the use of pharmaceuticals. Their study, like many others in the reconsolidation literature, follow a 3-day paradigm. On Day 1, participants were asked to memorize a list of objects (sock, tennis ball, pen, etc.). To do this, the experimenter would take each object out of the bag, show the object to the participant, ask the participant to name the object out loud, and then place it in a blue basket. Participants were given a memory test afterwards to make sure that they had encoded the information, are needed to recall at least 16 out of 20 (80%) of the objects before the session was over. If participants were unable to recall enough objects, the items were presented again in a similar fashion. On Day 2, participants were either reminded about the procedure on Day 1, or not. Participants who were in the reminder condition were asked “can you briefly describe what we did on Day 1?” but were stopped if they tried to name any specific objects from the original set. All participants then learned a second set of objects, but this time without the blue basket, so that it did not serve as its own reminder. On Day 3, a free recall memory test for set 1 was administered to both the reminder and no reminder condition. Results showed that participants who received a reminder about set 1 before learning set 2 made significantly more errors on the recall test. Specifically, those participants listed more words from set 2 when recalling set 1. These intrusions were considered evidence of reconsolidation as set 1 would have been reconsolidating during the time set 2 was being presented. However, because of the way reconsolidation was measured (only testing for information from set 1) some researchers attributed the results to source confusion.

Another study was conducted to counter the source confusion argument. Hupbach, Gomez, and Nadel (2009) looked at whether previous results could be explained using source confusion instead of reconsolidation. The experiment was largely similar to their previous experiment but with one critical difference. On Day 3, all participants (whether they received a reminder or not) took two separate free recall tests for items that were presented on Day 1 as well as Day 2. They found an asymmetrical intrusion pattern for participants in the reminder groups: words from List 2 were mistakenly thought of being from List 1 more often than List 1 words were mistakenly thought of being from List 2. This pattern of asymmetrical intrusions demonstrates that participants were not just making source errors, but that the original learning (List 1) was being updated with new information from the new set of information (List 2). Those in the no-reminder group did not show this effect and overall showed fewer intrusions from either list.

Many studies looking into the reconsolidation phenomenon (especially in the human episodic literature) have manipulated the kind of reminders that may or may not trigger reconsolidation. Some are explicit (like a verbal question asking about the original learning), but others are much more subtle. In another study using a 3-day paradigm, Forcato et al. (2007) used pairs of nonsense syllables, rather than physical objects to test the reconsolidation hypothesis. On Day 1, participants were instructed to memorize a list of syllable parings. On Day 2, participants were again split up into a reminder, or a no reminder group. Those in the reminder group were shown a single cue syllable from List 1 but before a response cue could be given, a notice appeared on the screen which announced that the session needed to be suspended. Afterwards, they went on the learn the second list of syllable pairings. Participants in the no reminder group learned the second list without getting a cue from List 1 and without seeing the notice about suspending the session. Despite the difference between the type of reminders, the results were similar to the results of Hupbach et al. (2007) in that participants who received a single cue from List 1 showed a resistance to retrieval induced forgetting[1], suggesting that the memory of List 1 had reconsolidated. These results also showed that reconsolidation applies not just to objects, but to verbal information as well. In addition, the authors suggested that prediction error played an important role in triggering reconsolidation as participants expected to be able to input a target syllable but were interrupted by the falsified computer error.

Although multiple studies have shown that reconsolidation can happen in episodic memory, it does not happen every time a memory is retrieved. Identifying the boundary conditions of episodic reconsolidation remains one of the greatest challenges to researchers in this field. Among the boundary conditions that have been suggested, one of the dominant hypotheses about what will trigger reconsolidation includes prediction error. Forcato, Argibay, Pedreira and Maldonado (2009) were among the first to test the necessity of prediction error in human episodic memory when triggering reconsolidation. In their study, 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 (like the procedure from the previous experiment) terminated the reminder portion of the experiment before learning List 2. The first group experienced this procedure but returned to learn List 2 after revisiting the same room the experiment took place in on Day 1.

[1] Retrieval induced forgetting is a memory phenomenon whereby memory performance is inhibited by the prior retrieval of other information from memory. This disruption usually occurs when the 'to-be' remembered information is related to the distractor information in some way.

The second group experienced the same context (just like the first group) and was presented with one cue syllable from List 1; however, the computer crashed before they had a chance to remember the target syllable and then they immediately moved on to learning List 2. The third group experienced the context from the first day and could respond to the cue before the computer crashed. On Day 3, each participant's memory for List 1 and List 2 was tested using cued recall. The results indicated that only the second group showed evidence of reconsolidation. The conclusion was that reconsolidation was only triggered when expectations were violated, and participants couldn't respond to the cue. This finding is akin 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).

Comparable to what Forcato found, not all reminders are successful in triggering reconsolidation. Hupbach et al. (2008) also manipulated different kinds of reminders and concluded that spatial context was among the most important. In this experiment, three conditions, each with a different reminder, were used as a method of reactivating previously encoded information. In the spatial context condition, the space that participants encoded the information in, served as the reminder and was held constant for List 1 and List 2. In the experimenter condition, the person running the experiment served as the reminder. Finally, in the question condition, participants were asked the question "Can you briefly describe the procedure from Day 1?". It is important to note that in each of these conditions, if a variable was held constant (like the spatial context or the experimenter), then all other variables were different. In the spatial context condition, there was a different experimenter on Day 1 and Day 2, and in the experimenter condition, participants learned the second set of information in a different spatial context. Participants in the questions condition were had both the experimenter and the spatial context changed between Days 1 and 2.

Intrusions from List 2 into List 1 were found in all conditions, but analysis revealed they were only significant in the spatial context condition. In this case, being in the same room as Day 1 on Day 2 served a reminder that triggered reconsolidation. Unlike the spatial context condition, participants in the question and experimenter conditions had relatively intact memory for the items from List 1, with significantly fewer intrusions from List 2. It is possible that special context is the key to triggering reconsolidation since other parts of a reminder could be built on top of the spatial context that they were originally encoded in. In this case, changing the spatial context would effectively remove the foundation for other parts of the memory. However, this idea is in conflict with those from Forcato et al., (2009), which show that despite all participants being in the same spatial context throughout the experiment, reconsolidation effects are only seen in certain conditions. Additionally, participants in the spatial context condition displayed evidence of reconsolidation despite not being subject to any kind of prediction error, which Forcato et al., (2009) suggested is key to triggering the effect.

The idea that the surrounding context could account for reconsolidation is not unique to spatial context. Sederberg et al. (2011) proposed that the temporal context model could also be used to explain reconsolidation even without the use of a consolidation-like process. The temporal context model can be broken down into three rules. First, encoding an item binds that item into the temporal context in which it was experienced. Second, retrieval of an item binds the current temporal context to the information recalled during test. Lastly, successful retrieval of an item at test also brings with it the temporal context in which the item was encoded. This is then used to update the current context for subsequent testing (Howard & Kahana, 2002). Sederberg et al. (2011) showed that applying the temporal context model to the 3-day reconsolidation paradigm could account for an asymmetrical pattern of intrusions since the target words on Day

1 would be bound to only the temporal context they were learned in. In contrast, the target words from Day 2 would be bound to the temporal context of Day 2, as well as the temporal context from Day 1, so long as a reminder of Day 1 is present. This yields a pattern of asymmetrical intrusions during test on Day 3 such that words from Day 2 are more likely to be mistakenly recalled as being learned on Day 1, since they share temporal context, whereas Day 1 words do not. It is possible that many reconsolidation effects in the literature could be explained using the temporal context model.

Reconsolidation as a State Dependent Phenomenon

To gain further clarity into the effect, some researchers have taken to looking at the reconsolidation phenomenon at the molecular level. Despite the name, research at a molecular level suggests that reconsolidation is not just a repeat of consolidation (Dudai, 2006). Because of the invasive nature of this type of research, all reconsolidation studies at the molecular level involve animals. In addition, most animal reconsolidation studies rely on a fear conditioning paradigm that is frequently paired with an injection of a protein synthesis inhibitor to show evidence of reconsolidation. The criteria for demonstrating reconsolidation in the animal paradigm is somewhat stricter than in the human literature; evidence of reconsolidation in animals requires evidence that a previously consolidated memory has been disrupted, and that in the absence of retrieval on Day 2, that same memory is unchanged even after the experimental manipulation (Tronson & Taylor, 2007). By injecting different protein synthesis inhibitors into regions of the brain thought to be associated with consolidation and reconsolidation, researchers are able to make inferences about which specific proteins contribute to the consolidation and reconsolidation processes (Nader, Schafe, & LeDoux, 2000; Duvarci, Mamou, & Nader, 2006; Eisenberg et al., 2003).

Despite growing evidence that reconsolidation is a unique cognitive phenomenon that, like consolidation, relies on protein synthesis, some researchers still believe that its effects could be explained using other pre-existing theories. Verrier et al., (2015) investigated the possibility that reconsolidation effects may instead reflect state dependent effects, which is the theory that memories bind to specific states when they are encoded, and therefore are retrieved more easily if the person is in a similar state during testing. Verrier et al., (2015) predicted that reconsolidation effects could be attributed not to a unique cognitive phenomenon, but instead to a lack of state consistency. The main idea is that when a memory is active, the internal state provided by an injection of a protein synthesis inhibitor is integrated within the initial memory and that any damage to that memory trace is a byproduct of the subject missing that internal state during testing. In their experiment, rats were injected with a protein synthesis inhibitor right after inhibitory avoidance training. Like other reconsolidation experiments, these rats displayed amnesic effects. However, these effects could be reversed when presented with a reminder, even when the reminder was another protein synthesis inhibitor. In addition, these results were replicated with the use of a chemical that does not affect protein synthesis. However, the most surprising finding was that a placebo that does not inhibit protein synthesis could recover a memory so long as that memory was novel, and the injection was presented just before acquisition or reactivation. Though this experiment focused more on consolidation than reconsolidation, the authors concluded that these results indicated that new memories can be established and maintained without protein synthesis and furthermore that the amnesic effects brought on by the inhibition of protein synthesis are due to an interruption of state dependent learning, and not by the disruption of a consolidation like process. To further relate their results to the reconsolidation phenomenon, additional experiments were conducted. In one, new chemicals (one known to inhibit protein synthesis and the other used as a control) were injected after reactivation of a previously consolidated memory. Results mimicked those of their first experiment, in that the memory deficit caused (presumably) by reactivating the original memory trace before injecting a protein synthesis inhibitor was reversed when the same chemical was given during test. Another experiment demonstrated that this effect was not time dependent, as the effects were seen even when the chemicals were injected 6 hours after memory reactivation. A result such as this could mean that many of the existing theories explaining reconsolidation are superfluous and that a majority of other study data could be explained using this state dependent hypothesis. However, this effect has yet to replicated or extended to human participants, which leads us to the current study.

The Current Study

Reconsolidation has received a lot of attention by researchers in the last 20 years, 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. So far, evidence of reconsolidation has been found in both animals and humans. However much of this evidence is not conclusive and a great deal of skepticism still exists regarding the reconsolidation phenomenon.

Verrier et al. (2015) raise some important questions for the reconsolidation literature that have not been answered in the human literature. The objective of the current study was to test the hypothesis that reconsolidation in the episodic memory system can be attributed to state dependent learning. Experiment 1 tested the state dependent hypothesis by changing the state of human participants via a mood induction procedure. Participants learned list 1 in a presumably neutral state (as they are when they enter the lab). Mood induction either occurred or not on Day

2 prior to learning the second list. Then, on Day 3 before testing occurred, participants again underwent a mood induction procedure (or not). Spatial context was held constant (in the lab) on all three days. The overall procedure was designed to be like Verrierr et al. (2015) in that participants would either be in a matching or mismatching state between study on Day 2 and test on Day 3. If the spatial context theory of reconsolidation is correct, participants in all conditions would have elicited reconsolidation effects due to the spatial context on all three days remaining constant (Hupbach et al., 2008). However, if reconsolidation is really a state dependent effect, as predicted by Verrierr et al. (2015), then only participants in conditions where their state is mismatched between days 2 and 3 would have shown an asymmetrical pattern of intrusions (a pattern indicative of reconsolidation). Instead, neither of these patterns were observed and participants only displayed reconsolidation effects in a single condition where state was matched on all three days and not just days 2 and 3.

Experiment 2 was designed with the outcome of Experiment 1 in mind. In Experiment 2, mood was manipulated from the start of the experiment (Day 1) for all participants. Rather than having all participants learn the first list in a neutral mood (Experiment 1), all participants learned List 1 after undergoing a mood induction procedure. The purpose of Experiment 2 was to attempt to replicate and confirm the post-hoc hypothesis from Experiment 1, but also to further generalize the effect of state dependency on reconsolidation.

Experiment 1

The purpose of Experiment 1 was to bridge the gap between some of the more recent and groundbreaking reconsolidation literature in the animal domain and the human one. Specifically, this experiment challenges the foundation of the reconsolidation hypothesis, which suggests that memories are brought into a labile state each time they are accessed (Przybyslawski & Sara, 1997). Instead, it could be the case that memories are state dependent and the results of many reconsolidation findings to date are not due to an interruption of the reconsolidation process, but instead are a side effect of changing the states between Day 2 learning and the Day 3 test (Verrier et al., 2015).

Method

Participants

Participants were 64 students (19 male, 45 female) recruited from the University of Nevada, Las Vegas. Participants were between the ages of 18 and 28 ($M = 19.60$). They were assigned to one of four conditions for a total of 16 participants per condition. Participants were randomly assigned to a mood induction or no mood induction group during the Day 2 study phase, and randomly assigned to one of those two groups during the test phase as well.

Materials

Materials from Kiley and Parks (submitted), which consists of two lists with 25 words each, were used. The words on each list were of middle to high frequency and were between 4 and 5 letters long. Lists were counterbalanced such that each list appeared in each condition (List 1 or 2) equally often across conditions. Words from each list appeared on screen using a desktop computer in the lab, which was used on all three days and for all conditions.

Mood induction materials from Baker and Guttfreund (1993) were used (Appendix A). While it is possible to elicit emotions via other more implicit methods (e.g. negatively valanced words or images), Bake and Guttfreund (1993) introduced an explicit method by asking participants to purposefully conjure negative emotions by calling to mind some of the most negative events in their life. It was hypothesized that this kind of method would allow for more individual differences, while still maintaining the validity of more traditional mood manipulation techniques. For neutral mood induction conditions, participants were instructed to read articles pertaining to the geography of various land masses taken from Wikipedia and answer various questions relating to how they felt while reading them (Appendices B and C).

Procedure

Participants came to the lab for three sessions that took place on three consecutive days not including Saturday or Sunday (Mon-Tues-Wed, Tues-Wed-Thur, or Wed-Thur-Fri). They were informed that they would be learning different lists and asked to recall them later. Participants took part in the study one at a time. Each participant signed an informed consent form before taking part in the study.

On Day 1, participants arrived in the lab; words were shown one at a time on screen for 2000 ms until the end of the list. Afterwards participants were asked to demonstrate knowledge of the list by typing in each word they remembered from List 1. If fewer than 20 words (80%) from the list were recalled correctly, the participant was asked to repeat the trial and List 1 was presented again in the same way as the first presentation, followed again by a free recall task. This cycle repeated up to a total of five times. If a participant failed to recall 80% of the list after the fifth attempt, the experiment concluded for that day and the participant was still instructed to return for the next day (they were only excluded if their accuracy on the final attempt was more than two standard deviations below the mean).

On Day 2, participants were split into two of the experimental groups. Half of the participants took part in the Autobiographical Recollection Induction Procedure (Baker & Guttfreund, 1993) to induce a mood state. Participants in these conditions read a two-paragraph instruction sheet that instructed them to spend 10 minutes reflecting on one of the saddest events in their life. They were asked to concentrate on an event that made them feel the most defeated, lonely, rejected, or hurt. The instructions indicated that they would be asked to answer several questions about the event to increase involvement in the task. The experimenter was not present in the room during this time to allow for improved reflection. After the 10 minutes had expired, participants answered broad, non-personal questions about the event (Where did this even occur? How old were you when this event occurred?). Afterwards, they began learning List 2 which was presented the same way as List 1. Those who were not in a mood induction condition for Day 2 were instead instructed to read a two-page article on a geographical region of the United States and asked to answer several questions about it after reading. After, they had finished reading and answering the questions, they began learning List 2, which was presented the same way as List 1. Participants were again asked to recall all words from the list and repeated the trial if under 80% of the words are correctly recalled. Just like Day 1, a maximum of five trials were attempted.

On Day 3, we further split participants into two conditions, creating a 2x2 design for the experiment overall. Half of the participants took part in the mood induction procedure before continuing to the test portion of the experiment. The mood induction procedure was identical to what was used during Day 2. If participants were not in the condition with mood induction before the final test, they were instructed to read a two-page article on a geographical region of the United States and asked to answer several questions about it. This article differed in content from the one given to participants not in the mood induction condition on Day 2. After the previous task was completed, all participants were instructed to recall both lists from the previous days via a free recall test for each list independently. They did not get to see the words again. It is important to note that the presentation of List 1 and List 2, was counterbalanced, but List 1 (whichever set of words that happened to be), was always tested first. This creates a more conservative estimate of the reconsolidation effect, as we are most interested in the intrusions made from List 2 into List 1, and presenting List 2 at test first, could prime some participants to make those intrusions later, thereby potentially capturing an effect other than reconsolidation.

Results – Experiment 1

Acquisition Performance Days 1 and 2

Accuracy for the immediate recall tests given on Day 1 and Day 2 was measured to ensure criterion for those days was met and that accuracy on days 1 and 2 did not vary by condition. All participants reached at least 80% accuracy on days 1 and 2. The number of attempts required for each participant to reach criterion was recorded and analyzed. On Day 1, participants took an average of 2.64 learning trials to reach criterion. On Day 2, participants took an average of 2.37 learning trials to reach criterion. There were no differences between any of the conditions for either day. A two-way analysis of variance (day-2 mood x day-3 mood) was conducted to compare the number of trials between lists across all conditions. There were no significant effects (all p's > 0.05).

Free Recall Day 3

A 2x2 ANOVA (mood Day 2 by mood Day 3) that was used to analyze day-3 recall performance for List 1 and List 2 did not reveal any differences between conditions, List 1: $F_{(3,}$

$_{63)}$ = 1.17, p =.327; List 2: $F_{(3, 63)}$ = 1.74, p =.167. However overall differences in accuracy between the lists was significant $t_{(63)}$ = -3.61, p < .01. List 1 M = 10.74, List 2 M = 13.32, with higher recall for Day 2.

Asymmetrical Intrusion Effect

The main variable of interest, the asymmetrical intrusion effect, was calculated by creating a difference score between the number of intrusions from List 2 → 1 and List 1 → 2. This number is used here to indicate a reconsolidation effect, where a greater positive number indicates a larger effect and implies that the memory from Day 1 was made labile and therefore susceptible to updating from the events of Day 2 (List 2). The asymmetrical intrusion effect was analyzed using a two-way ANOVA (Day 2 mood by Day 3 mood) (See Figure 2). The interaction term was significant $F_{(1, 60)}$ = 5.83, p = .019, η_p^2 = .09, indicating that the asymmetrical intrusion score was highest when mood was the same on Day 2 and Day 3. Post-hoc analyses indicated that the asymmetrical intrusion score was only significantly different from 0 when participants were kept in a neutral mood state on both Day 2 and Day 3 $t_{(15)}$ = 2.67, p = .017. This suggests that reconsolidation only occurred in this condition.

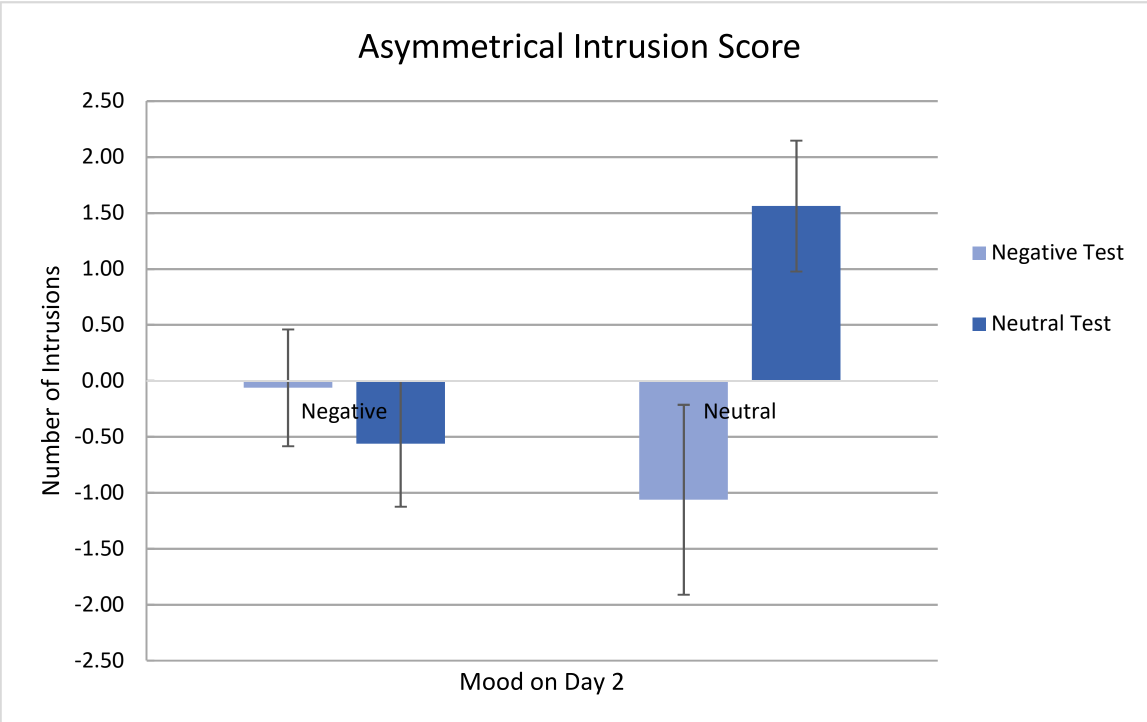

Figure 2: Asymmetrical Intrusion Score as a function of mood on Day 2 and Day 3 in Experiment 1

Discussion - Experiment 1

State-dependent learning would predict that reconsolidation should only be found when Day 2 and Day 3 are mismatched, while current reconsolidation theory would suggest either a positive asymmetrical intrusion effect in all conditions due to spatial context being held constant, or in no conditions, due to prediction error being necessary. Here, we show neither of these patterns. Instead we demonstrated a reconsolidation effect only in the condition where mood was neutral on both Day 2 and Day 3. Crucially, it is also the only condition where mood was kept constant across all three days of the experiment since mood was neutral on Day 1 across all conditions. Because of this, it is possible that reconsolidation could still be a state dependent phenomenon as some of the animal literature suggests, but that state must match during all three days of the experiment. Due to this unexpected pattern of results, Experiment 2 was conducted to help test the explanation of these conclusions.

Experiment 2

Experiment 2 was designed to test the hypothesis that the effects of reconsolidation can be mediated by matching states on all three days. This experiment manipulated mood in a similar way to Experiment 1, but rather than all participants going through Day 1 without a mood induction procedure, they started with a negative Day 1 instead. This difference notwithstanding, Experiment 2 follows the same procedure as Experiment 1. Beyond just replicating the state dependent hypothesis, Experiment 2 was also designed to confirm that the results from Experiment 1 were not due to the negative state itself rather than the overall differing states between the conditions.

Method

Participants

Participants were 64 (23 male, 40 female, one student identified as agender) students recruited from the University of Nevada, Las Vegas. Participants were between the ages of 18 and 31 (M = 19.47). They were assigned to one of four conditions for a total of 16 participants per condition. Participants were randomly assigned to a mood induction or no mood induction group during the Day 2 study phase, and randomly assigned to one of those two groups during the test phase as well.

Materials

Materials from Experiment 1, including the words lists and mood induction materials, were used. Lists were counterbalanced such that each list appeared first in each condition (List 1 or 2) equally often across conditions. Words from each list appeared on screen using a desktop computer in the lab, which was used on all three days and for all conditions.

Procedure

Participants came to the lab for three sessions that took place on three consecutive days not including Saturday or Sunday (Mon-Tues-Wed, Tues-Wed-Thur, or Wed-Thur-Fri). They were informed that they would be learning different lists and asked to recall them later. Participants took part in the study one at a time. Each participant signed an informed consent form before taking part in the study.

On Day 1, participants arrived in the lab; and were exposed to the same mood alteration procedure from Experiment 1 to induce a mood state. All participants completed the mood alteration procedure on Day 1 regardless of condition. After the mood alteration procedure, participants learned the first word list. Words were presented in the same fashion as in Experiment 1. Afterwards participants were asked to demonstrate knowledge of the list by typing in each word they remembered from List 1. If fewer than 20 words (80%) from the list were recalled correctly, the participant was asked to repeat the trial and List 1 was presented again in the same way as the first presentation, followed again by a free recall task. This cycle repeated up to a total of five times. If a participant failed to recall 80% of the list after the fifth attempt, the experiment concluded for that day and the participant was still instructed to return for the next day (like Experiment 1, they were only excluded if their accuracy on the final attempt was more than two standard deviations below the mean).

On Day 2, participants were split into two of the experimental groups. Half of the participants again induced a negative mood state within themselves using the Autobiographical Mood Induction Procedure. This procedure was identical to the one used in Experiment 1. Those who were not in a mood induction condition for Day 2 were instead instructed to complete the neutral task. This neutral task was also identical to the one used in Experiment 1. After they had finished with either the negative or neutral procedure, they began learning List 2. List 2 was presented the same way as List 1. Participants were again asked to recall all words from the list and repeated the trial if under 80% of the words were correctly recalled. Just like Day 1, a maximum of five trials were attempted.

On Day 3, we further split participants into two conditions, creating a 2x2 design for the experiment overall. Half of the participants took part in the mood induction procedure before continuing to the test portion of the experiment. The other half completed the same neutral task from Day 2, but with a different article to read. After the previous task was completed, all participants were instructed to recall both lists from the previous days via a free recall test for each list independently. They did not get to see the words again. Akin to Experiment 1, List 1 (whichever set of words that happened to be), was always tested first. This creates a more conservative estimate of the reconsolidation effect, as we are most interested in the intrusions made from List 2 into List 1, and presenting List 2 at test first, could prime some participants to make those intrusions later, thereby potentially capturing an effect other than reconsolidation.

Results – Experiment 2

Acquisition Performance Days 1 and 2

Accuracy for the immediate recall tests given on Day 1 and Day 2 was measured to ensure criterion for those days was met and that accuracy on days 1 and 2 did not vary by condition. All participants reached at least 80% accuracy on days 1 and 2. The number of attempts required for each participant to reach criterion was recorded and analyzed. On Day 1, participants took an average of 2.91 learning trials to reach criterion. On Day 2, participants took an average of 2.55 learning trials to reach criterion. There were no differences between any of the conditions for either day. A two-way analysis of variance (day-2 mood x day-3 mood) was conducted to compare the number of trials between lists across all conditions. There were no significant effects (all *p's* > 0.05).

Free Recall Day 3

A 2x2 ANOVA (day-2 mood x day-3 mood) was used to analyze day-3 recall performance for both lists and did not reveal any differences between conditions, List 1: $F_{(3, 60)} = 0.31$, $p = 0.82$; List 2: $F_{(3, 60)} = 0.76$, $p = 0.52$. However overall differences in accuracy between the lists was significant $t_{(63)} = -5.13$, $p < .01$. List 1 $M = 10.63$, List 2 $M = 13.94$, with higher overall recall for Day 2.

Asymmetrical Intrusion Effect

When discussing the main variable of interest, the asymmetrical intrusion effect, it is important to keep in mind that mood on Day 2 and Day 3 were the main IV's, but that mood was negative for all participants regardless of condition on Day 1. The AIE was again calculated by creating a difference score between the number of intrusions from List 2 → 1 and List 1 → 2. As before, a greater positive number indicates a larger effect and implies that the memory from Day 1 was susceptible to updating from the events of Day 2 (List 2). The asymmetrical intrusion effect was analyzed using a two-way ANOVA (day-2 mood x day-3 mood) (See Figure 3). There was a significant effect of day-2 mood $F_{(3, 60)} = 4.80$, $p = .032$, $\eta_p^2 = .07$, but not of day-3 mood ($p > .05$). The interaction term was also non-significant ($p > .05$). This result indicates that participants who were in a negative mood state on Day 2 before learning the second list of words had a higher AIE score than those who were in a neutral state during Day 2. This result was primarily driven by participants who were not only in a negative mood state during Day 2, but during Day 3 as well. A single sample two-way t-test was run on all conditions to help confirm this. As hypothesized, only the condition where participants were kept in a negative state during all three experiment days had an AIE score significantly different from 0 $t_{(15)} = 2.60, p < .05$).

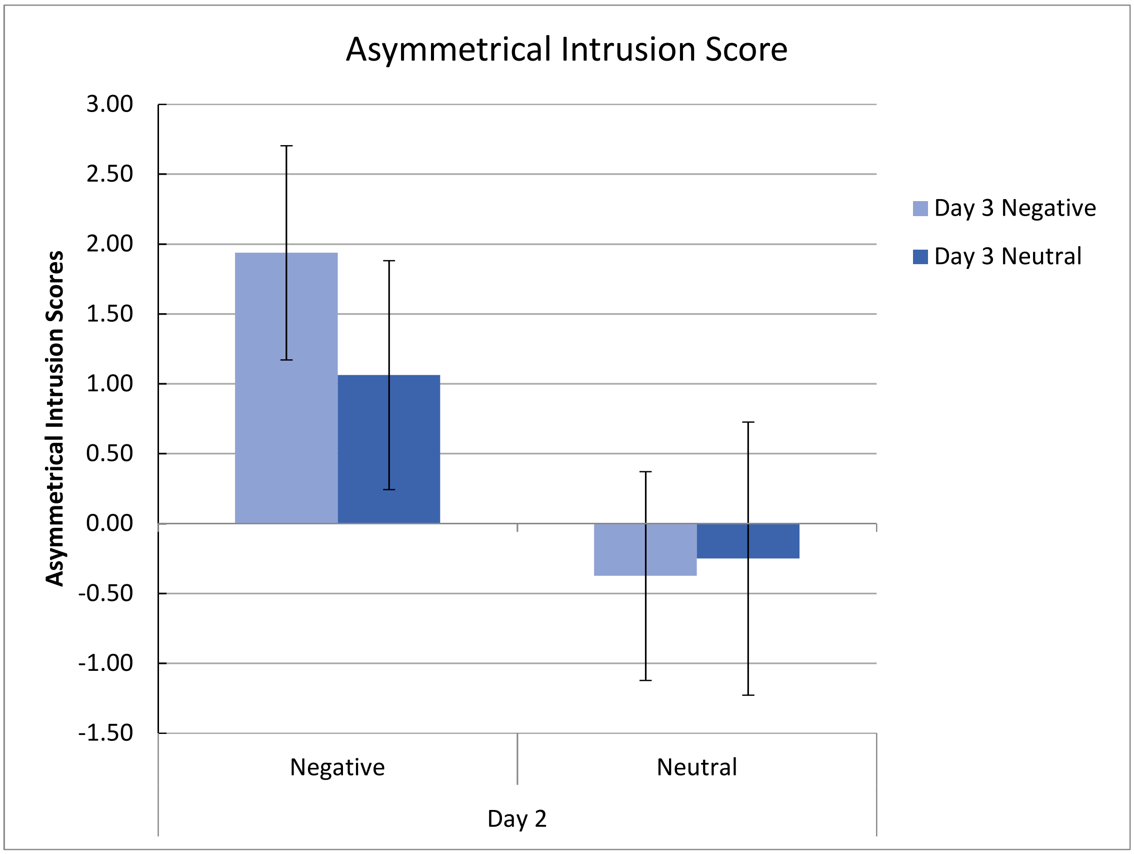

Figure 3: Asymmetrical intrusion scores for Experiment 2. All participants in a negative mood state during Day 1

Discussion - Experiment 2

There were two crucial differences between Experiment 1 and Experiment 2. First, mood manipulation was introduced on Day 1 in Experiment 2, rather than on Day 2 like it was in Experiment 1 where participants were considered to be in a neutral state for mood purposes but did not complete any kind of neutral task. Second, in Experiment 2, Day 1 was considered to be a negative day for all participants, regardless of condition.

Experiment 2 was designed to test the hypothesis created based upon the results of Experiment 1; not only that reconsolidation is not only triggered by similar states on Day 1 and 2, but that in order to observe a pattern of results similar to previous reconsolidation studies (asymmetrical intrusions), participants need to be in a similar state during testing as well. Like the results of Experiment 1, the results of Experiment 2 do not line up with any of our a priori hypotheses regarding reconsolidation. Verrier et al. (2015) would predict that reconsolidation be found only when Day 2 and Day 3 are mismatched. This idea comes from the state dependent literature and while this may apply to rats who are exposed to protein synthesis inhibitors, the same does not seem to apply to human emotional states. Similarly, other theories of reconsolidation such as Hupbach's spatial context hypothesis (Hupbach et al., 2008) or Pedreira's theory behind the necessity of prediction error (Pedreira et al., 2004), also do not fit with the current pattern of results. However, it is worth noting that while we can say for certain that spatial context was kept constant across all three days, it may be harder to control for the presence of subjective prediction error within our conditions.

Despite what previous research has shown, we demonstrated a reconsolidation effect only in the condition where mood was negative on all three days. It may be the case that the term "reconsolidation effect" may not be the most appropriate here, since the pattern of results found in both Experiment 1 and 2 can mostly be explained via the temporal context model. However, the temporal context model doesn't provide a perfect explanation either. The temporal context model suggests that memories are bound to their context during encoding and would predict that participants who were in the same mood on days 1 and 2, but not Day 3, would not be able to isolate words from List 1 since List 1 would have been tied to the context from days 1 and 2, whereas List 2 would only be tied to Day 2. However, the participants in the condition that followed this pattern of mood manipulation, did not exhibit evidence of reconsolidation, suggesting that context must be shared during test (as well as the both study days) for the effects of reconsolidation to be measurable.

General Discussion

Ultimately, the pattern of results found in Experiment 1 and 2 is novel within the reconsolidation literature. Here, we find that reconsolidation did not occur as hypothesized. Participants did not make significant asymmetrical intrusions when they learned both lists in the same spatial context, or when participants were in different emotional states on Day 2 and 3. Instead, only participants who were in the same state (regardless of whether that state was neutral or negative) on all three experiment days showed evidence of reconsolidation.

Previous research has shown that when rats were exposed to a chemical designed to block reconsolidation after re-exposure to a known stimulus, they failed to recall that stimulus during a later memory test (Verrier at al, 2015). This phenomenon is well documented in the reconsolidation literature. However, rats that were injected with the same chemical right before testing experienced no negative effects from the first dosage and were able to recall the original stimulus as well as controls who were not exposed to the chemical at all. This led Verrier et al. (2015) to conclude that reconsolidation effects in the animal literature may be due to a mismatch of state, since rats who are exposed to the blocker during encoding of a stimulus associate that stimulus with the chemical. Because the chemical is not introduced during testing, the rat is unable to use the same context to aid in recall, resulting in what appears to be genuine memory loss. In the current study, we created a mismatch of state through emotional manipulation in an attempt to replicate these state dependent effects. Though our results do not necessarily contradict the findings of Verrier et al. (2015), because of the myriad of differences in study design (rats and pharmaceuticals, as well as the manipulation of Day 1 state), our lack of reconsolidation effects in conditions where participants were in the same state on Days 2 and 3 (but a different state on Day 1) make it harder to equate their findings to human declarative memory. However, our results here do indicate that state effects are important to the reconsolidation phenomenon, but unlike the results of Verrier et al. (2015), our results suggest that state effects only play a role when state is the same during all 3 days. However, if we consider the major differences between the typical human and animal protocols, it is possible that our results do not necessarily conflict with Verrier et al. (2015) at all. While many animal and human studies have two separate study sessions, animals in reconsolidation experiments only learn or interact with one stimulus, whereas human participants learn two sets of stimuli. It is possible that state dependency only plays a role when state is consistent for each presented stimulus.

In the currently study, we cannot be certain that conjuring negative memories did not provide participants with extra context with which to bind the lists to. Regardless, our results here contradict the findings of Hupbach et al. (2008) as well as Kiley and Parks (submitted). In previous reconsolidation studies, evidence of reconsolidation is found when spatial context is held constant across all three days, but not if it differs. In the current study, spatial context wasn't manipulated, and was the same across all three days, which should have resulted in evidence of reconsolidation in all conditions.

As previously stated, the current results do not map onto any current reconsolidation theories and while it is still possible that reconsolidation is a novel cognitive phenomenon, given these results it seems more likely that it can be explained using one or more existing cognitive theories. The current literature provides several alternative explanations for the reconsolidation hypothesis beyond just that it is a new cognitive phenomenon. It is entirely possible that theories such as state dependent learning, or the temporal context model (Sederberg et al. 2011) already give us adequate explanations of the effect seen in much of the reconsolidation literature. It may be time to accept the possibility that reconsolidation is not a novel memory phenomenon, and instead that it can be explained using theories that already exist in the human episodic memory literature.

Appendix A: Autobiographical Mood Induction Procedure

I would now like to ask you to take a few minutes to look into your past and think about what have been the two saddest events in your life. When you finish reading these instructions, take 5-10 minutes to think of these events. I will tell you when the time is over. I would like you to try and think of all the details of what was happening at the time, to the point that you could imagine this happening to you right now. This about how old you were, who were the people or events involved, and what your feelings were.

When the time is over, I will ask you to answer a few questions related to the images you thought of. It is very important that you take this reflection exercise seriously. Think of those events that made you feel lonely, rejected, defeated, or hurt. Please sit back, close your eyes, put your head down, or get into a position that will best allow you to get in touch with your feelings. Take your time and think about these sad events. Start now.

The following are the written questions given after the induction procedure:

	Event one	Event two
Approximately how old were you at the time of the event?		
In what city did this happen?		
Which was the sadder of the two? (Please make a check under the event).		

Appendix B: Neutral Article 1

The eastern United States has a varied topography. A broad, flat coastal plain lines the Atlantic and Gulf shores from the Texas-Mexico border to New York City, and includes the Florida peninsula, which is home to some of the most beautiful beaches in the world. This broad coastal plain and barrier islands make up the widest and longest beaches in the United States, much of it composed of soft, white sands. The Florida Keys are a string of coral islands that reach the southernmost city on the United States mainland (Key West). Areas further inland feature rolling hills, mountains, and a diverse collection of temperate and subtropical moist and wet forests. Parts of interior Florida and South Carolina are also home to sand-hill communities. The Appalachian Mountains form a line of low mountains separating the eastern seaboard from the Great Lakes and the Mississippi Basin. New England features rocky seacoasts and rugged mountains with peaks up to 6200 feet and valleys dotted with rivers and streams. Offshore Islands dot the Atlantic and Gulf coasts.

The five Great Lakes are located in the north-central portion of the country, four of them forming part of the border with Canada, only Lake Michigan situated entirely within United States. The southeast United States, generally stretching from the Ohio River on south, includes a variety of warm temperate and subtropical moist and wet forests, as well as warm temperate and subtropical dry forests nearer the Great Plains in the west of the region. West of the Appalachians lies the lush Mississippi River basin and two large eastern tributaries, the Ohio River and the Tennessee River. The Ohio and Tennessee Valleys and the Midwest consist largely of rolling hills, interior highlands and small mountains, jungle marsh and swampland near the Ohio River, and productive farmland, stretching south to the Gulf Coast. The Midwest also has a vast amount of cave systems.

The Great Plains lie west of the Mississippi River and east of the Rocky Mountains. A large portion of the country's agricultural products are grown in the Great Plains. Before their general conversion to farmland, the Great Plains were noted for their extensive grasslands, from tallgrass prairie in the eastern plains to shortgrass steppe in the western High Plains. Elevation rises gradually from less than a few hundred feet near the Mississippi River to more than a mile high in the High Plains. The generally low relief of the plains is broken in several places, most notably in the Ozark and Ouachita Mountains, which form the U.S. Interior Highlands, the only major mountainous region between the Rocky Mountains and the Appalachian Mountains.[6][7]

The Great Plains come to an abrupt end at the Rocky Mountains. The Rocky Mountains form a large portion of the Western U.S., entering from Canada and stretching nearly to Mexico. The Rocky Mountain region is the highest region of the United States by average elevation. The Rocky Mountains generally contain fairly mild slopes and wider peaks compared to some of the other great mountain ranges, with a few exceptions (such as the Teton Mountains in Wyoming and the Sawatch Range in Colorado). The highest peaks of the Rockies are found in Colorado, the tallest peak being Mount Elbert at 14,440 ft (4,400 m). In addition, instead of being one generally continuous and solid mountain range, it is broken up into a number of smaller, intermittent mountain ranges, forming a large series of basins and valleys.

West of the Rocky Mountains lies the Intermontane Plateaus (also known as the Intermountain West), a large, arid desert lying between the Rockies and the Cascades and Sierra Nevada ranges. The large southern portion, known as the Great Basin, consists of salt flats, drainage basins, and many small north-south mountain ranges. The Southwest is predominantly a low-lying desert region. A portion known as the Colorado Plateau, centered around the Four Corners region, is considered to have some of the most spectacular scenery in the world. It is accentuated in such national parks as Grand Canyon, Arches, Mesa Verde and Bryce Canyon, among others. Other smaller Intermontane areas include the Columbia Plateau covering eastern Washington, western Idaho and northeast Oregon and the Snake River Plain in Southern Idaho.

The Intermontane Plateaus come to an end at the Cascade Range and the Sierra Nevada. The Cascades consist of largely intermittent, volcanic mountains, many rising prominently from the surrounding landscape. The Sierra Nevada, further south, is a high, rugged, and dense mountain range. It contains the highest point in the contiguous 48 states, Mount Whitney (14,505 ft or 4,421 m). It is located at the boundary between California's Inyo and Tulare counties, just 84.6 mi or 136.2 km west-northwest of the lowest point in North America at the Badwater Basin in Death Valley National Park at 279 ft or 85 m below sea level.[8]

These areas contain some spectacular scenery as well, as evidenced by such national parks as Yosemite and Mount Rainier. West of the Cascades and Sierra Nevada is a series of valleys, such as the Central Valley in California and the Willamette Valley in Oregon. Along the coast is a series of low mountain ranges known as the Pacific Coast Ranges.

Alaska contains some of the most dramatic and untapped scenery in the country. Tall, prominent mountain ranges rise up sharply from broad, flat tundra plains. On the islands off the south and southwest coast are many volcanoes. Hawaii, far to the south of Alaska in the Pacific Ocean, is a chain of tropical, volcanic islands, popular as a tourist destination for many from East Asia and the mainland United States.

Appendix C: Neutral Article 2

Located in the north, west and east latitudes of the Northern Hemisphere, most of Russia is much closer to the North Pole than to the equator. Individual country comparisons are of little value in gauging Russia's enormous size and diversity. The country's 17.09 million square kilometers include one-eighth of the Earth's inhabited land area. Its European portion, which occupies a substantial part of continental Europe, is home to most of Russia's industrial activity and is where, roughly between the Dnieper River and the Ural Mountains, the Russian Empire took shape. Russia includes the entire northern portion of Asia.

From west to east, the country stretches from Kaliningrad (the exclave separated by the 1990 Re-Establishment of the State of Lithuania from the then-Soviet Union) to Ratmanov Island (one of the Diomede Islands) in the Bering Strait. This distance spanning about 6,800 kilometers (4,200 mi), to Nome, Alaska. From north to south, the country ranges from the northern tip of the Russian Arctic islands at Franz Josef Land to the southern tip of the Republic of Dagestan on the Caspian Sea, spanning about 4,500 kilometers (2,800 mi) of extremely varied, often inhospitable terrain.

Extending for 57,792 kilometers (35,910 mi), the Russian border is the world's longest. Along the 20,139-kilometer land frontier, Russia has boundaries with 14 countries: Norway, Finland, Estonia, Latvia, Lithuania, Poland (via the Kaliningrad Oblast), Belarus, Ukraine, Georgia, Azerbaijan, Kazakhstan, Mongolia, the People's Republic of China and North Korea. Approximately two-thirds of the frontier is bounded by seawater. Virtually all of the lengthy northern coast is well above the Arctic Circle; except for the port of Murmansk—which receives currents that are somewhat warmer than would be expected at that latitude, due to the effects of the Gulf Stream—that coast is locked in ice much of the year. Thirteen seas and parts of three oceans—the Arctic, Atlantic, and Pacific—wash Russian shores.

The Russian Arctic stretches for close to 7,000 kilometers (4,300 mi) west to east, from Karelia and the Kola Peninsula to Nenetsia, the Gulf of Ob, the Taymyr Peninsula and the Chukchi Peninsula (Kolyma, Anadyr River, Cape Dezhnev). Russian islands and archipelagos in the Arctic Sea include Novaya Zemlya, Severnaya Zemlya, and the New Siberian Islands. About 57 percent of Russia is tundra—a treeless, marshy plain. The tundra is Russia's northernmost zone, stretching from the Finnish border in the west to the Bering Strait in the east, then running south along the Pacific coast to the northern Kamchatka Peninsula. The zone is known for its herds of wild reindeer, for so-called white nights (dusk at midnight, dawn shortly thereafter) in summer, and for days of total darkness in winter. The long, harsh winters and lack of sunshine allow only mosses, lichens, and dwarf willows and shrubs to sprout low above the barren permafrost. Although several powerful Siberian rivers traverse this zone as they flow northward to the Arctic Ocean, partial and intermittent thawing hamper drainage of the numerous lakes, ponds, and swamps of the tundra. Frost weathering is the most important physical process here, gradually shaping a landscape that was severely modified by glaciation in the last ice age. Less than one percent of Russia's population lives in this zone. The fishing and port industries of the northwestern Kola Peninsula and the huge oil and gas fields of northwestern Siberia are the largest employers in the tundra. With a population of 180,000, the industrial frontier city of Norilsk is second in population to Murmansk among Russia's settlements above the Arctic Circle. From here you can also see the auroras (northern lights).

Taiga the most extensive natural area of Russia - stretches from the western borders of Russia to the Pacific. It occupies the territory of the Eastern Europe and West Siberian plains to the north of 56 ° -58 ° N and most of the territory east of Yenisei River taiga forests reach the southern borders of Russia in Siberia taiga only accounts for over 60% of Russia. In the north-south direction the eastern taiga is divided (east of the Yenisei River), with a continental climate, and west, with a milder climate, in general, the climate zone is moist, moderately warm (cool in the north) in the summer and harsh winter, there is a steady snow cover in the winter. In the latitudinal direction, the taiga is divided into three subzones - northern, middle and southern taiga. In the western taiga dense spruce and fir forests on wetlands alternate with pine forests, shrubs, and meadows on the lighter soils. Such vegetation is typical of the eastern taiga, but it plays an important role not fir and larch. Coniferous forest, however, does not form a continuous array and sparse areas of birch, alder, willow (mainly in river valleys), the wetlands - marshes. Within the taiga are widespread fur-bearing animals - sable, marten, ermine, moose, brown bear, Wolverine, wolf, and muskrat.

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