# THE ROLE OF RHYTHMIC BRAIN ACTIVITY IN LONG TERM MEMORY RETRIEVAL

by

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A THESIS

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This study aims to elucidate the relationship between Working Memory (WM) and Long Term Memory (LTM) on a neurological basis. In WM tasks, it has been well documented that the alpha frequency signal (8-12 Hz) occurs at the onset of the stimulus. This study seeks to answer whether or not a similar neural pattern exists during a LTM task when the subject retrieves spatial information and holds it in mind. Additionally, when does this signal occur? I predicted that the alpha signal would reoccur upon retrieval of the spatial stimuli thus revealing a re-representation into working memory. To get at these hypotheses, participants (N=27) participated in a LTM task over the course of two days. Day 1 involved the studying of various objects' spatial location on a circular array. On day 2, participants were tested on the items and their brain activity recorded. Results revealed that the alpha signal (8-12 hz) indeed did occur upon retrieval of the spatial representation from LTM. The signal occurred at approx. 600 ms and was sustained through the remainder of the trial. These findings suggest that Spatial Working Memory and holding spatial info in mind retrieved from Long Term Memory rely on the same neural mechanism.

# Acknowledgements

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# Introduction

## Defining Memory

How can something that one utilizes and needs for everyday functioning be so poorly understood? Memory is much more complex than simply the process of remembering; that is merely the surface concerning the full-range of memory functions and capabilities. Past empirical data and behavioral experiments have allowed for the development of cognitive theories and the distinguishing of memory processes. For example, the American Psychological Association now defines memory as: "The mental capacity to encode, store, and retrieve information" (2014). Essentially, memory formation follows a three-step process: the encoding or receiving of information, storage of this encoded information, and finally the actual recollection of that information. However, such experiments and simplistic definitions are only the beginning and do not acknowledge the brain as memory's biological substrate. Cognitive-neuroscience aims to elucidate this definition and begin to understand just what is occurring in the brain during these processes. The end goal being the developmentof a "neural-map" that can merge the gap between theory (i.e. different types of memory) and underlying neural mechanisms. With improved technologies, the vague understanding of memory will continually evolve and no longer will memory descriptions need to be rooted in observed behavior. As a result, research requires constant refinement by psychologists and scientists alike. They must employ a cycle between empirical research and theoretical mechanisms in order to understand the interlinkagesof memory's unique yet simultaneous processes.

To that end, memory is modernly divided into two, primary theoretical categories: Working and Long-Term Memory. Working Memory (WM) refers to the transient storage and manipulation of information (Baddeley 1992), and Long Term Memory (LTM) is information that is retained for an enduring period of time (Gazzaniga et. al 1998). The overall discernment between LTM and WM proves increasingly difficult as these functions occur simultaneously and continually. For example, consider recalling an event that occurred a week ago. The recall or "remembering" involves LTM processes while the current representation in mind (the "remembered representation") relies on the mechanisms concerning WM. The inverse is also true; information cannot bypass initial decoding and awareness (WM processes) to be stored as a LTM. They are continually in sync. This difficulty cements the need for continual research and refinement in order to understand this relationship and thus isolate the underlying mechanisms for just what is occurring in the brain as someone retrieves a memory. As LTM is the primary focus of this study, it is necessary to outline its two subdivisions: declarative and non-declarative. Non-declarative refers to knowledge we no longer have conscious access to (e.g. riding a bike). It is closely associated with "semantic memories" in literature (Tulving 1998). Semantic memory refers to the display of certain knowledge without any recollection of obtaining that knowledge. In contrast, declarative refers to information that one has the conscious knowledge of (i.e. one is aware of their own personal knowledge or autobiography). It is also closely related to "episodic memories" (a polar to semantic) in that one maintains an "episode" of when certain events occurred or how the knowledge was attained (i.e. the story behind the memory, fact, event etc.) (Tulving 1989). Declarative (conscious)

LTM is the focus of this study as the experiment relies on exact retrieval of previously learned stimuli; as well as participants possessing the awareness that they studied and have access to this particular stimulus (specific experimental methods will be extrapolated in subsequent sections).

**Relevant Cognitive Neuroscience Background**

The above definition of memory merely presents its primary functions: the encoding, storing, and retrieving of memories. While this definition fails to map these specific roles onto subdivisions of memory and the constituents of the brain, it serves as a foundation to meticulously expand upon. As previously noted, research supports divisions (distinguished by type and role) within the memory system (Macdonald 2008). Certain areas of the brain are believed to be associated with these divisions in the memory system: the temporal lobe (forms and strengthens new memories), the prefrontal cortex (encodes and retrieves), and the temporal cortex (stores memories). If the focus is Long-Term Memory (LTM) and its eventual retrieval, how is it stored initially? Information in WM becomes a LTM through consolidation. Consolidation, in this context, refers to stabilizing a memory after its initial acquisition (Macdonald 2008). This typically involves the repetition of this knowledge or stimulus in addition to creating meaningful associations/connections (Carrier et. al 2003). This is the process participants will undergo in the experiment at hand.

What is occurring physiologically during this consolidation? The hippocampus is involved with the strengthening of a memory from WM to LTM (Kesner RP 2013). Research suggests the hippocampus may have a role in the dynamic nature of neural connections up to three months or more after initial acquisition of the memory (Kesner RP 2013). Essentially, when knowledge (or a stimulus) is presented, various neurons "fire" and are aroused. During acquisition, and the subsequent learning/rehearsal, neural networks in the brain (circuits of neurons) "communicate." This communication and connection between neurons is known as the firing of nerve synapses (structures that allow neurons to pass information to other neurons). An important distinction to note is that neuron synapses are also involved in WM. However, it is the augmenting of this repetition that distinguishes it from WM and thus solidifies this knowledge as a LTM. This entire process is modernly referred to as "Long-Term Potentiation" (LTP). LTP is the extension of "Hebb's Law" which states: "if a weak and strong input act on a cell at the same time, the weak synapse becomes stronger" (Gazzaniga et. al 1998). In other words, neurons that fire together, wire together (Sadananda 2012). This reveals that neurons function in a group and can be strengthened and/or trained. This is particularly useful in our study where retesting and testing allows the subject to strengthen those neurons that "fire" for a certain stimulus (this notion will be further related to the experiment in methodologies). While this describes how a memory is consolidated from WM to LTM, what about the reverse? Consider a "pathway analogy" to visualize a respective neuron circuit. In strengthening these neural synapses, a familiar "pathway" is created for this information. This path is a "two-way street" between WM and LTM and thus allows for activation from pillar to post. When stimulated, these neurons fire and bring the information from "storage" to WM awareness. This phenomenon, and the underlying mechanisms concerning retrieval, is the aim of the study.

## Frequencies

In order to properly understand the subsequent data, it is important to examine the specific neural frequency bands. As previously noted through the Hebb's law, neurons that fire together, due to their preference for a certain stimulus (e.g. color, spatial, etc.), wire together and strengthen. This allows a previously learned stimulus to activate the group of neurons (neuron circuit) that were initially activated and consolidated through initial acquisition. This synchronized arousal of neurons is manifested through an oscillation at a certain frequency. These resulting frequencies are distinguished as respective, neural bands. Specifically, Theta and Alpha bands correspond to rhythmic oscillations of 4-7 Hz and 8-12 Hz respectively (Jensen et al., 2002). Research has associated recognition and recollection of previously learned information with the "Alpha" band of neurons in WM (Rihs et. al 2006; Worden et al., 2000; Yamagishi et al., 2005; Thut et al., 2006). Further, a study by Khaderet. al (2010) examined both WM and LTM in conjunction: "the more effort within the WM system (increased memory load) supports successful LTM encoding. Thus, the same neural processes underlying WM maintenance support LTM encoding. This research suggests that Alpha has a prominent role in LTM, decoding, and retrieval. Alpha has also been suggested to inhibit "distractors" in the rehearsal stage of consolidating items into WM (Jiang et. al 2010).

## Tracking the Contents of Working Memory

In order to discuss the potential of tracking the contents of Long Term Memory (LTM), it is important to discuss the literature in Working Memory (WM). How can one track the contents of any type of memory? The answer to this begins with the notion of the Sensory Recruitment Hypothesis (SRH). Details are represented in WM via the recruitment of the same neural structures that encoded the stored info. In other words, the SRH allows us to keep specific, detailed info about a stimulus in mind. For example, if two lines with different angle orientations are shown (e.g. 45 and 135 degrees), FMRI studies (i.e. the recording of blood flow in the brain) reveal multi-voxel patterns of activity are represented through a series of varying data or vectors (Serences et. al 2009). Specifically, the voxels represent a neuron firing at a rate for that particular orientation. Because the patterns were different for the orientations, yet in the same brain region, this notion of multi-voxel classification supports the idea of recruiting neural structures and creating an active representation via previously stored encoding. This activity was further able to discern a color through patterns in the "what" region of the brain while the "where" was revealed in the upper dorsal. Two separate features (color and orientation) showed different patterns in different areas thus allowing one to "read" someone's mind and determine stimulus specific info of a given object (i.e. discern two different things about an object as its two facets of memory). In short, one can estimate the degree to which each voxel is responding to each of the stimuli.

This same concept is extended to EEG literature. Electrodes measure the power of the bands at different locations on the scalp (electrodes centered over different regions). These electrodes provide the values or vector (similar to the voxel paradigm). Unlike the voxels, however, these values were encoded via EEG analysis. In looking at EEG-based Channel Tuning Functions (CTFs), the spatial distribution of EEG power at the identified frequency contained reliable information concerning the orientation of the stimulus (able to encode what was “in mind”) (Garcia et al 2013). During the delay period of a WM task, the goal is look at the ongoing neural activity, which is associated with storage. In so doing, one can decode stimulus specific activity related to neural processes. As aforementioned, it has been continually postulated that neurons representing items in WM are synchronized with specific frequency bands (Lisman&Idiart, 1995) (Raffone and Wolters 2001). In this analysis, it is the alpha frequency band (8-12 Hz) that revealed a constant effect throughout the delay period of the task thus associating the alpha band with WM. This analysis revealed a method for tracking memory precision with “near real-time” temporal precision. It also showed that neural activity related to WM is manifested in alpha frequency band synchronization. The above analysis described is known as Fourier analysis and will be utilized in creating and analyzing Channel Tuning Functions (CTF) in this LTM experiment.

**Foundational Research**

Recent literature serves as the catalyst for this study. Research by Rihs and colleagues (2007) suggests that Alpha is highly associated with spatial Working Memory (WM) as their study evoked strong alpha oscillations during the encoding process (act of memorization); thus, the alpha band can reveal the focus of spatial attention. Additionally, it is possible to track the contents of WM (spatial) through alpha band activity (Foster et. al in prep). This previous research reveals the need to include long-term memory focused experiments to attempt to refine the mapping of frequency bands to the memory system.

## General Research Questions

The research question at hand is twofold in nature as it relies on the complementary results of both EEG and behavioral data. On one hand, the question seeks to clarify the relationship between Long Term Memory (LTM) and Working Memory (WM). Theoretically, the processes are continuous and not mutually exclusive, and thus EEG data should reflect that. In other words, processes associated with WM, at some point in a LTM task, should be activated and replicated. With previous data associating alpha signals with WM encoding, it would be beneficial to elucidate this in a LTM task to gain insights concerning similarities or differences in the underlying neural mechanisms responsible. Are the mechanisms the same? In retrieving a memory, what is the nature of this representation? Is it identical to WM only tasks? Will Alpha come back on and when? Further, from the behavioral data, what kind of conclusions can one draw from the repeated study and consolidation of objects spatially? Do participants improve in overall recollection and precision? If so, by how much? What does this imply concerning the nature and relationship between LTM and WM? The study aims to gain insight on such questions through a LTM task that incorporates the consolidation of WM into LTM. It accomplishes such consolidation through studying various objects and their subsequent retrieval the following the day.

# Methods

## Participants

Thirty participants aged 18- 35 completed the study. Three participants were excluded due to excessive EEG artifacts (described below) leaving 27 subjects whose data were analyzed. Participants received monetary compensation ($10 per hour). Based on self-report, all participants had normal or corrected-to-normal vision. They gave informed consent in accordance with regulations set by the University of Oregon and the Institutional Review Board.

## Methods Summary

The task took place over the course of two, consecutive days. On day 1, participants signed a consent form and were given detailed instructions about the task. They then learned a series of clipart images and their respective position for approximately two hours. On day 2, participants were tested over the same objects while their brain waves were being recorded for approximately 3 hours. Subjects were then debriefed on the experiment.

## Stimuli

For the tasks, 120 unique, clipart images were collected through a google search. These images were all recognizable objects/silhouettes as opposed to abstract shapes (see Fig. 1). These images were all a consistent teal color (please note that the object is black in Fig. 1 for clarity purposes but all objects were teal), so that only spatial position and object identification were required to successfully complete the task.

**Task Specifications**

The task was generated through MATLAB using the Psychophysical Toolbox Extension, which was displayed from a 17-inch, flat, cathode ray tube computer screen. Stimuli were rendered against a gray screen, and this computer featured a refresh rate of 120 HZ. Participants sat approximately 100 cm away from the screen. Stimuli were presented as a series of 120 different clip art images all of which were a teal blue. Each clipart position was presented with a unique position within the 360-degree space. There were 960 trials in all (8 blocks of 120 trials).

*Day 1*

Each trial began with a space bar bush. A blank display appears at a variable length between 800-1500 ms.This was followed by a single image, centered in the screen, which subjects viewed for 1 second. This second allowed for participants to tell exactly what it was. The object then moved to its position for half a second. This was done 10 images at a time and followed by a testing period of the preceding ten items (Roediger and Karpicke 2006). In the testing period, image order was randomized in order to mitigate the Recency Effect (Holbrook 2008). Additionally, the object was presented in the center of a 360-degree array, and the subject was asked to click on the correct position of the array. The ring and centered image were on screen for one second before the cursor appears. During this one-second, participants were asked to keep their eyes centered and not to move them to the anticipated response location.This was to ensure proper recording of the retrieval process without interference from eye and muscle movements. Response was not timed and feedback was given immediately and appeared for 500 ms (e.g. -30 if the subject was 30 degrees to the left from the correct position). This continued for all 120 images (10 at a time, test on each 10 in random order for a total), and was then followed by a testing period of all 120 at the conclusion, which was also randomized and featured the same specifications (e.g. object presented for one second). This process is repeated twelve times for the 120 objects for a total of two hours. Participants signed up for the part two EEG/Capping experiment the following day.

*Day 2*

After learning the objects during day 1, subjects came back in and were capped and prepped for EEG recording (please see the subsequent "Collection and Artifact Rejection" for precise EEG recording procedures). The task was comparable to the testing phase of day 1 as they were tested on all 120 objects in a random order. This was repeated 8 times (however, some subjects only had time to complete 7 rounds of testing). Similar to the first day, the task began with a space bar push and then a blank screen for 800-1500ms (varied). The recall cue was then presented for 1250 ms (object appeared centered in the 360 degree array) (See Fig. 1). Subjects were asked to remain fixated on the object and not move their eyes nor think about where they were going to respond (subjects who did move their eyes/impede on collection were removed). Subjects were asked to retrieve all 120 items in a random order 8 times for a total of 960 trials. Detailed information about collection and rejection will be discussed in the subsequent section. Participants then responded by clicking on the remembered position of the array and were once more given feedback in degrees.

## EEG Collection and Artifact Rejection

EEG data were collected using the lab's standard recording and analysis procedures. This includes the rejection of trials where blinks and large eye movements hinder the data. The recording was done through twenty-two, tin electrodes mounted in an elastic cap (Electro-Cap international) and utilized the International 10/20 system. All sites were recorded with a left-mastoid reference, and the data were referenced, and the data was re-referenced offline to the algebraic average of the left and right mastoids. Horizontal electro-oculogram (EOG) was recorded from electrodes placed approximately 1 cm to the left and right of the external canthi of each eye to measure horizontal measures. The EEG was amplified with an SA instrumentation amplifier with a bandpass of .01-80 Hz and were digitized at 250 HZ in labVIEW 6.1 on a PC. In order to detect blinks, vertical EOG was recorded from an electrode mounted beneath the left eye and referenced to the left mastoid to detect eye movements. Subjects data were included only if they had 550 artifact free trials. 3 subjects were excluded for excessive artifacts.

## Channel Tuning Functions

As previously mentioned, recent computational advances allow for the decoding of the aggregate measure of electrophysiological scalp measurements. Specifically, researchers can decode the various cortical regions' respective orientation selectivity through the Forward Encoding Model (Brouwer and Heeger 2009). EEG electrodes act as sensors that read the non-uniform distribution of orientation-selective cells. This allows for the classification of neural responses. Through this applied model, one can summate the orientation-selective responses. These responses yield the average activity measured by each electrode.  The spatially global sensors are able to measure alpha waves as the sensors reveal the aggregate measure of neural activity in a group of cells.

Data featuring stronger amplitudes (as measured by sensors) will reveal the cells that prefer a given orientation. This is known as orientation selectivity. For example, consider a spatial representation at 90 degrees. The group of neurons that prefer a 90-degree orientation will fire strongly for 90 degrees and that effect will slowly reduce the farther the orientation moves from 90. An example of this is evident in a study by Garcia and colleagues (2013). The researchers were able to show above-chance classification of stimulus values. These values were based on the response profiles created by the sensors and reflecting the specific neural firing patterns for various stimuli. Essentially, the different activity relevant to unique orientations allows one to accurately portray the population code. In this case of this experiment, the same logic applies to neurons firing for specific spatial locations.

Neural population codes are used to simplify the raw, orientation-specific responses. Specifically, populations codes divides the 180 degrees into 8 channels each pertaining to unique 22.5 degrees. These channels are “bins” which represent spatial preferences in the channel tuning functions. If the x-axis plots the spatial preference, then one can assume that the 8 channels each produce their own, unique tuning function relevant to the neural preference. These tuning functions look like bell-curves or traditional distributions (the peak of the amplitude referring to the peak arousal for a population of neurons and then diminishing the farther away from the peak). The forward encoding model (Brouwer and Heeger 2009) is used to obtain a summation of the 8 Channel Tuning Functions. This model assumes that each neural response is the product of the weighted, linear sum of 8 tuning functions where the peak amplitude is centered over the preferred stimulus channel. This pattern (i.e. a distribution where the peak is centered and diminishes from left to right) is the primary reason for presenting the data from each channel together. This conceptual overview of CTF's sets the foundations for the following results section and how one can analyze and represent EEG frequencies for a specific stimulus.

**Mixture Modeling**

While Channel Tuning Functions allow EEG data to be represented and analyzed, a mixture-model is relevant in analyzing the behavioral data (Zhang & Luck 2008). Specifically, this model fits the two types of possible responses (guess and remembered) of a given participant across all trials. This model shows the probability of selecting each spatial location on the 360 degree array (+/- 180) for each object. In order to so, the model must include the probability of the participants guessing on any given trial in relation to correct responses (probability of retrieval) as well as the range of responses for an item in memory centered around 0 (mnemonic precision). Guessing refers to having the object not in memory and thus having equal likelihood of selecting every spatial location (including the correct one). In this way, the mixture model (Zhang & Luck 2008) accounts for the flat distribution expected as a response for an object not in memory. As a mixture model combines guess and remembered responses, standard estimation is employed to arrive at the components separately (i.e. probability of having the item in memory and probability of a guess). Probability of retrieval (the likelihood of an "in memory" response) is then derived from subtracting the guesses from the total number of responses (calculated as the vertical onset from the uniform guess distribution or flat line). In other words, the flat line, representing equal distribution of a guess, and the tall curve representing responses in memory are collapsed across trials and form one bell curve. Even with the object in memory, the representation is not perfect. As such, precision is calculated by how many degrees the response was from the correct position for an object that is in memory (e.g. if the participant chose the 190 degree location for an object studied at 170 degrees, 30 degrees is the precision). In this experiment, a response error histogram for one subject illustrates the mixture of objects in memory and not in memory (see Fig. 2). Specifically, the histogram shows an average of one participant's responses in relation to the correct response across all trials (correct spatial location represented as 0 degrees). Essentially, the mixture model attributes performance error to the differences in memory representations and gives rise to the behavioral measures reported and discussed in subsequent sections.

# Results

## Hypothesis

In order to cater to the breadth of aforementioned research questions, I generated a hypothesis for both behavioral and EEG data. From a performance perspective, I hypothesized that participants would become both more accurate and precise in identifying objects and remembering their respective spatial locations as the task progressed. This would be due to the repeated studying and testing on the objects. This hypothesis is partially based on the knowledge of the “testing effect” as supported in recent findings by Roediger and Karpicke (2006).

Previous literature has revealed the role of the alpha frequency during Working Memory (WM) Tasks (Rihs et. al 2007), so I hypothesized that a Long Term Memory (LTM) task would reflect the shift from a LTM retrieval to a WM representation based on the return of the alpha signal. In other words, I hypothesized that during Day 1 studying/testing, objects were being studied in WM and consolidated into LTM. After retrieval, WM and thus the alpha signal, are back online while the object is held in mind to complete the task. The holding in mind of reconstructed LTM representations should invoke an alpha signal similar to that of a WM task. If my hypothesis holds true, results will confirm WM’s association with the alpha signal while elucidating the relationship between WM and LTM. Further, it provides a timeline of the retrieval process (i.e. the approximate time needed to retrieve an object's spatial information from LTM).

## Behavioral Data

### *Probability of Retrieval*

Probability of retrieval refers to the participant's ability to accurately recognize and place an object. After 7 blocks of 840 trials, participants were able to correctly identify nearly all of the objects (See Fig 3). There were 8 blocks in all, but not all participants were able to complete 8 in the time constraint. Thus, the subsequent data will only report on 7 blocks for standardization purposes. As such, accuracy was recorded and averaged across the 7 blocks and participants had a 90 percent chance of accurately retrieving the object from LTM ($M$= .90, $SD$= .11). Overall, probability of recall increased by 12.6 percent. Individual averages and standard deviations were recorded for each Block in order to examine the differences within subjects (e.g. Block 1 ($M$=82.5%, $SD$=12%) through Block 7 (M=94.5%, SD=8.6%)). This reveals a positive, linear relationship between number of blocks and probability of recall.

### *Mnemonic Precision*

As previously mentioned in the methodology and probability of retrieval, subjects received feedback in degrees concerning their precision of response (e.g. a feedback of -30 if they were off 30 degrees to the left). A feedback of 0 indicated a perfect response in the 360-degree response array. Across all subjects, the average mnemonic precision was within approximately 13.5 degrees with a standard deviation of 4.87 for the combined 7 blocks (See Fig. 4). Overall, precision increases by about 4.11 degrees after completing 7 blocks.  As with probability of retrieval, individual averages were obtained for each block (e.g. Block 1 (*M*=16.3, *SD*=8.2) through Block 7 (*M*=12.2, *SD*=4.33)). These values refer to the average deviation of every participant in a specific block as opposed to all blocks combined. Comparable to probability of recall, results reveal a positive relationship between number of blocks and precision. However, unlike probability of recall, which consistently increases with each block progression, there is little to no improvement in precision between Blocks 4-7.

**EEG Data**

The resulting Channel Tuning Function reveals an induced, aggregate alpha signal across all electrodes at approximately 600 ms into the task (See Fig. 5). This is during the retrieval portion of Day 2 testing (See Fig. 1). This signal remains activated and consistent throughout the 1000 millisecond recording time per trial (Fig. 5).

## Discussion

I hypothesized that the alpha response typical of Working Memory (WM) tasks would also occur during a Long Term Memory (LTM) task. Specifically, that this signal return would correspond with the active representation held in mind that was retrieved from Long Term storage.  This was proven to be true as an alpha signal is invoked and sustained midway through the retrieval component of the task. Specifically, it occurs at approximately 600ms. This differs from spatial WM Tasks that provide an alpha response immediately after the onset of a stimulus(Rihs et. al 2006; Worden et al., 2000; Yamagishi et al., 2003; Thut et al., 2006). The observed alpha signal return in an LTM task has several implications on the understanding of memory. The first being that this study replicates the alpha frequency's role in spatial WM rehearsal.This is due to the similar alpha response in memories containing specific spatial information that are held in mind from LTM and WM rehearsal tasks. Evidently then, alpha responses are associated with active maintenance of stimuli, which is something that occurs in both WM and LTM retrieval tasks. However, this alpha response is invoked immediately in WM tasks and later in LTM spatial tasks. This suggests holding spatial information in mind retrieved from LTM (at approx. 600 ms) and spatial WM rely on similar neural mechanisms. Thus, it is intuitive that holding items in mind retrieved from LTM is re-activating WM processes.  In other words, LTM involves retrieving a memory and re-representing it in WM to invoke the same response that occurs immediately in WM tasks. The observed Alpha spike is thus indicative of the completed retrieval and the onset of a reconstructed spatial, WM representation. This study provides evidence for the complementary nature or "pathway" between spatial LTM and WM on a neurological basis. Finally, because the signal is delayed for approximately 600 ms, this allows one to estimate how long it takes to retrieve a spatial memory.

The study presents many follow up questions and future directions. There is little research studying LTM in isolation as it is incredibly difficult to isolate LTM and WM. However, this study provides a novel insight on its retrieval. Particularly, the length of time required to retrieve a spatial memory. This study is one of the first to show the onset of the alpha signal as synonymous to the end of LTM retrieval. In addition to elucidating the relationship between LTM and WM on a neural level, it provides quantitative insights and a methodology that will help fuel future experiments. Particularly, experiments that test LTM retrieval times with a variety of different stimuli and features. This study examined the neural activity post retrieval/the maintenance of a LTM, spatial representation. A logical follow up is designing experiments that examine the retrieval period itself. What exactly is occurring in the brain before that 600 ms mark? Is a different frequency band induced? This will help uncover a neural mechanism for the actual remembering of the stimuli. There has been a large emphasis on the notion that this pertains only to spatial LTM. It would be beneficial to extend research to a variety of features and complexities. This will help elucidate the relationship between the frequency bands and memory processes. Just how associated are specific frequency bands with a certain type of memory? Are they not at all and rather solely feature dependent? Is it a combination of both? Further, this experiment serves as a catalyst for further research in examining the time of retrieval. The overall average was approximately 600 ms, but what attributes individual variances in retrieval time? Is it Working Memory capacity or IQ differences? Further, does time of retrieval vary not only within subjects but also within trials and why? Are memories that are more precise more quickly recalled? Finally, is retrieval time dependent on feature? In other words, would one expect a similar time for retrieving color or other features from LTM? Additional research is needed to address these new questions generated from this study.

My hypothesis was also supported in the accuracy and precision of participants' performance. In both the "probability of recall" and "mnemonic precision" conditions, subjects improved across trials. There was a positive, linear relationship in probability of recall as subjects had nearly a 95 percent chance of correctly recalling an object by the final block. With each progression, performance improved which replicates the efficacy of the Testing Effect. Testing oneself on the material is truly the best way to remember material as the participant would have intuitively acquired 100 percent probability of recall if trends continued. Considering the large amount of items, this is an impressive feat and has generalizable implications concerning how one approaches studying and academia. The positive and effective results from testing periods changes the way society views testing. It is no longer just a means of assessment but also an incredibly effective way to learn (and prepare for such assessment). Precision also improved as a function of repetition and progression. It would be valuable for further research to test just how many blocks/tests are needed to attain perfect retrieval for this amount of objects. At what amount of objects or features would the testing effect begin to diminish for? This would help researchers acquire insights into the capacity limits of LTM rehearsal. However, unlike probability of recall, results were relatively stagnant after the third block. This suggests that precision of memories is more difficult to improve or increase and that LTM spatial representations may have a precision threshold around 12 degrees. The data suggests that precision would remain around 12 for every block after 7. This has broad implications concerning the limitations on our memories and how precise they can be. Further research is needed to examine this trend or perhaps reflect a similar threshold. From a societal standpoint, does a lack of precision reveal the need for skepticism in human accounts such as eyewitness testimony? Or is the precision threshold a minor detail that does not impact memories enough for them to prove invalid? Further research is needed to address such questions.

The overarching goal of this experiment, and similar literature, is to bridge the gap between neural mechanisms and mental processes. The end goal being a "neural map" of memory processes which would allow full understanding and association between neural activity and observed phenomena. How can a phenomenon like memory, that is so essential, and constantly occurring, be so poorly understood? If the sects of memory function as a holistic process, you must first dissect and attempt to isolate each for improved understanding. With this heightened understanding, this research provides potential implications for the clinical treatment and interventions of neurological disorders (e.g. in order to fix a car engine, you must understand each part, how it works, and how it works together). Understanding these relationships may also refine certain therapies based on the wiring and association of neurons in addition to enhancing or creating other therapies for cognitive or memory disorders. Further, the creation of a neural map that has associated neural frequencies to brain functions provides many benefits. One could examine discrepancies in those frequencies whichreveals malfunctions in the brain. This could serve as the catalyst for pharmaceuticals that are able to manipulate various areas of the brain and neural activity responsible for various cognitive functions.

# Figures

Figure 1: Task Figure for “Day 2” EEG Testing with Relevant Times (ms)

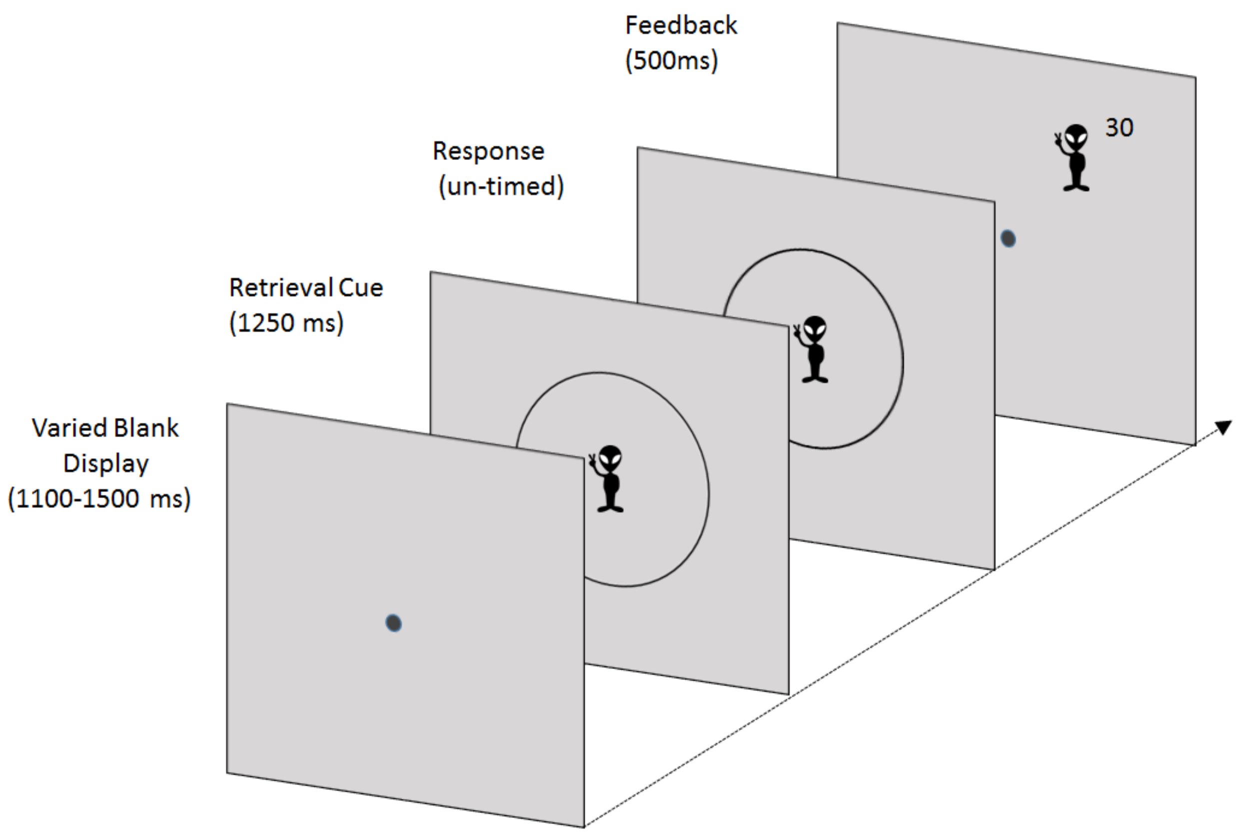


Figure 2: Response Error Histogram Representing a Mixed Model

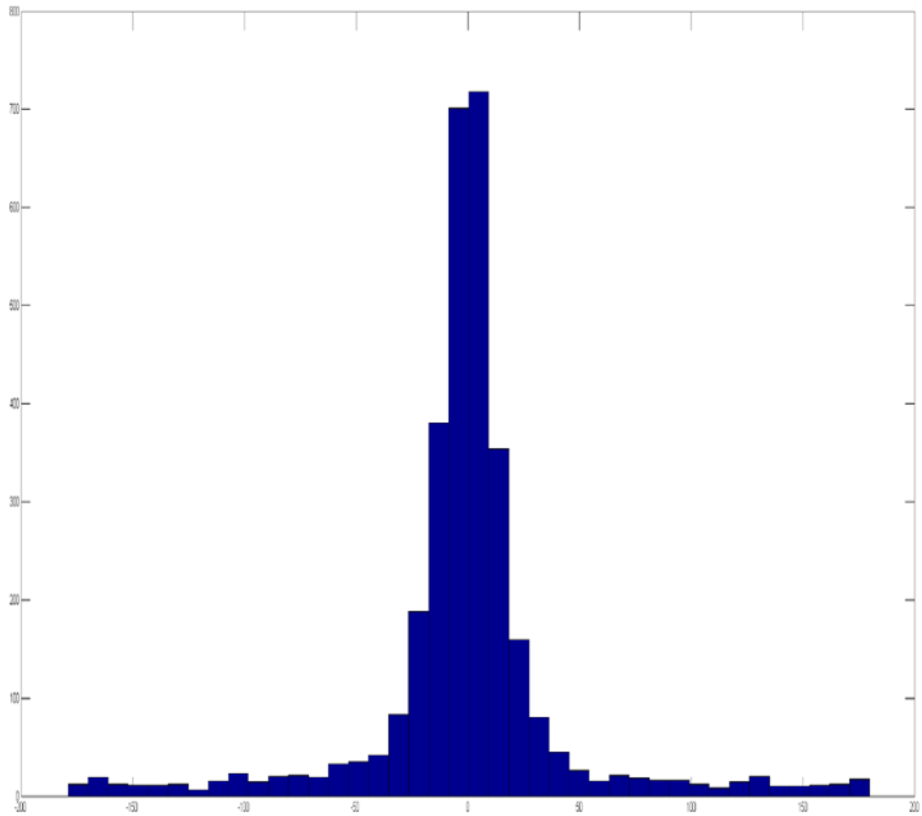


Figure 3: Behavioral Data for Probability of Recall as a Percent

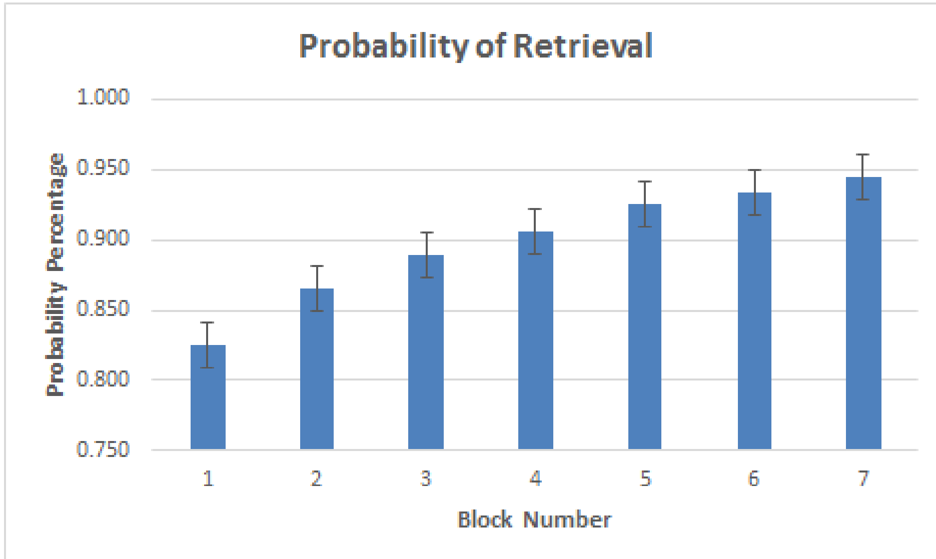



Figure 4: Behavioral Data for Mnemonic Precision (SD)

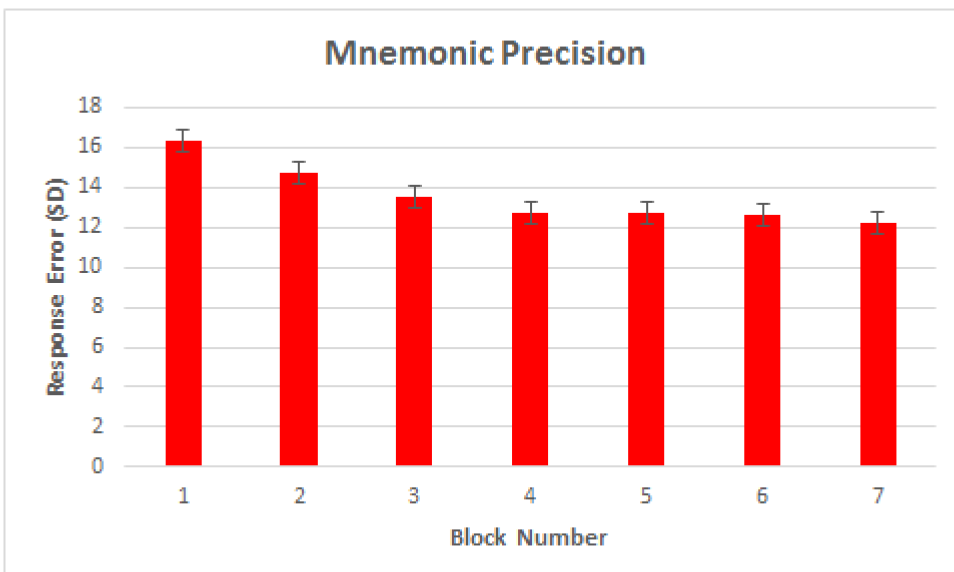
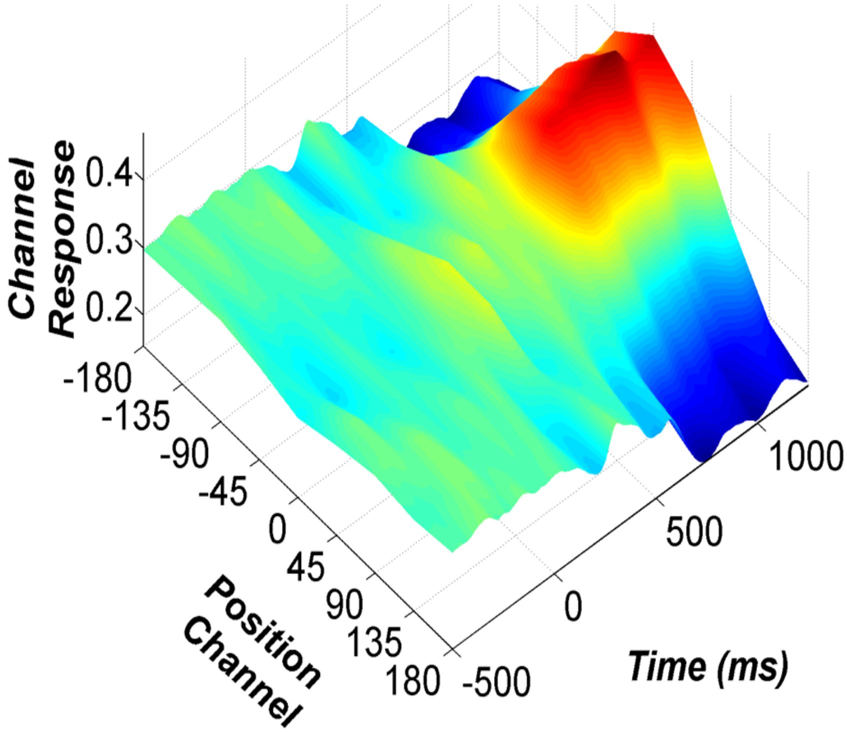


Figure 5: Average Alpha (8-12 Hz) Channel Tuning Functions for all participants observed in EEG Testing



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