An Exploration of Failures in Visual Working Memory: A Steady-State Visual Evoked Potential Study

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Abstract

Working memory consists of three stages: encoding, maintenance, and retrieval. It has been demonstrated that working memory (WM) capacity is limited to about four items (Cowan 2001). However, there are ambiguities regarding why some items are correctly retrieved and why others are subsequently lost. Previous studies have not been able to demonstrate at which stage these items are lost because these studies only measure the processing of all items shown in a memory array. This investigation employs a novel paradigm pairing frequency tagging and a full report paradigm. This paradigm allowed us to disentangle individual items that were encoded and compare these items to the items that were actually retrieved. Two attentional models were tested in regards to encoding: the ‘graded attention’ model and the ‘all or nothing’ model. These two models describe how neural resources are allocated to items in a memory array. This study found that frequency tag amplitudes were larger for items correctly retrieved as compared to items subsequently forgotten. The data were also found to be consistent with the ‘all or nothing’ attentional model that states that attentional resources are spread to all items during encoding. The results indicate how important WM encoding is to explaining underlying mechanisms for why WM fails.
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# Table of Contents

**Introduction** ...............................................................................................................................................................................1

Background: Testing WM in a Laboratory Setting .........................................................................................................................2

Role of Attention in WM ...................................................................................................................................................................3

Role of WM Maintenance .................................................................................................................................................................4

Full Report Versus Partial Report ................................................................................................................................................6

Frequency Tagging Technique .........................................................................................................................................................6

Approach and Aims .............................................................................................................................................................................10

**Methods** ......................................................................................................................................................................................12

Participants .....................................................................................................................................................................................12

Stimulus Apparatus and Display ....................................................................................................................................................12

Electrophysiological Apparatus and Recordings ...........................................................................................................................13

Task Design and Procedure ............................................................................................................................................................13

Behavioral Data Analysis ...............................................................................................................................................................17

Electrophysiological Data Analysis .............................................................................................................................................18

**Results** .....................................................................................................................................................................................22

Behavioral Accuracy .......................................................................................................................................................................22

Frequency Tag Amplitude During WM Encoding .........................................................................................................................25

**Discussion** .................................................................................................................................................................................29

Current Investigation and Goals ......................................................................................................................................................29

Implications ......................................................................................................................................................................................31

**References** .................................................................................................................................................................................33

**Appendix** ..................................................................................................................................................................................39
List of Tables

Table 1: Participant demographics........................................................................................................39
Table 2: Individual participant accuracy..................................................................................................40
Table 3: Index values for individual participants .....................................................................................41
List of Figures

Figure 1: Testing working memory in a laboratory setting ........................................3
Figure 2: Attentional models and expected frequency tags .......................................9
Figure 3: Stimuli shown during experiment .................................................................14
Figure 4: Visual working memory task design .............................................................16
Figure 5: Visualization of analysis .............................................................................20
Figure 6: Electrode cluster selection .........................................................................21
Figure 7: Behavioral working memory accuracy .......................................................23
Figure 8: Response order accuracy ...........................................................................24
Figure 9: Percentage of trials with x items recalled ....................................................25
Figure 10: Average index values for each electrode cluster and condition .................27
Figure 11: Electrode placement and topographic maps ............................................28
List of Formulas

Formula 1: Frequency-based index value........................................................................38
Introduction

Every person has had an instance when he or she needs to store a phone number in his or her brain and correctly recall the digits of that phone number in order to call someone. However, when he or she goes to retrieve the phone number, he or she has already forgotten it. Forgetting a phone number over a period of a few seconds reflects a failure in working memory (WM) (Uylings, Van Eden, De Bruin, Corner & Feenstra, 1990). Specifically, one of the three stages of WM has failed. The first stage, encoding, describes the initial perception of the item going into WM (Uylings et al., 1990). In the case of remembering a phone number, encoding involves using one’s vision or hearing to encode the phone number. If an individual has a failure of attention while reading or listening to the phone number, then he or she would fail to encode the phone number. The second stage, maintenance, describes storing information over a short period of time. In WM, the individual stores information over a period of a few seconds. With regard to remembering a phone number, maintenance involves the person cognitively storing the digit array in his or her brain. A failure in storing the digits results in a maintenance stage failure. The third stage, retrieval, involves accessing the information provided during encoding. In regards to remembering a phone number, the individual may experience a failure in retrieval, as he or she cannot correctly remember the correct digits of the phone number. WM failure may occur during encoding, maintenance, or retrieval.

Because WM plays an integral role in daily cognition, it is important to understand the mechanisms underlying why WM fails. As such, the aim of this thesis is geared towards understanding the role of encoding in WM.
Background: Testing WM in a Laboratory Setting

Working memory (WM) can be described as information that a person can temporarily access and manipulate while completing a cognitive task (Wheeler & Triesman, 2002). The amount of information someone can temporarily access is described as WM capacity and is known to be limited to approximately four items (Cowan 2001). People use WM to assist in everyday cognitive activities such as remembering a phone number. When an individual is given a phone number, this person must store the digits in his or her brain for access at a later time. WM is separated into three distinct stages: encoding, maintenance, and retrieval. Researchers use computer-generated experiments to test WM capacity limitations and modulate WM processes. As such, the current investigation uses a computer-generated program. In the laboratory setting, the three stages of WM are studied with computer-generated programs, as visualized in Figure 1.
Role of Attention in WM

Previous studies have attempted to elucidate reasons why WM fails. One of these reasons may be attention (Rouder, Morey, Morey, & Cowan, 2011; Adam, Mance, Fukada & Vogel, 2015; Rouder, Morey, Cowan, Morey & Pratt, 2008). Attention describes how humans integrate important stimuli in their environment, yet ignore other perceptible stimuli (Anderson 2005). In order to encode an item, a participant must first have attention on that item (Awh, Vogel & Oh, 2006). Hence, if attention fails, then WM fails (Ikkai & Curtis, 2011). There are different models of attention, which describe failures in WM. One model, called the ‘all or nothing’ model, states that a participant will either remember all items shown in a stimulus array or no items, as a result of either attending or not attending to an item (Rouder et al., 2011). The alternative model, ‘the
graded attention’ model, states that attention is graded depending on a participant’s WM capacity which can be defined as the amount of information someone can temporarily access (Adam et al., 2015). High WM capacity individuals have better sustained attention than low WM capacity individuals. As such, these high WM capacity participants remember more items in a stimulus array than low WM capacity participants.

Rouder et al. (2008) has supported the ‘all or nothing’ model. However, this study used a partial report paradigm (e.g. probe a single item at retrieval) that depends on an aggregate number of trials. Partial report paradigms probe a single item for retrieval and hence, do not provide a comprehensive measure regarding which items are actually encoded or why attention fails. When a full report paradigm that tests every stimulus item was used, the results support the ‘graded attention’ model (Adam et al., 2015). As a full report probes all items from a memory array, more information is provided about how many items a participant actually remembers on a trial-by-trial basis. As such, a full-report paradigm is used in the present investigation.

**Role of WM Maintenance**

Some studies attempt to disentangle the neural mechanisms underlying the stage of WM failures but have focused primarily on the maintenance stage of WM (Funahashi, Bruce, & Goldman-Rakic, 1990; Fuster & Alexander, 1971; Todd & Marois, 2004; Xu & Chun, 2006; Vogel & Machizawa, 2004; Magen, Emmanouil, McMains, Kastner, & Treisman, 2009). These studies have shown that across measures of neural activity (e.g. functional imaging and electrophysiology), there is a period of heightened neural activity during encoding that is sustained through maintenance during WM tasks. In both primates and humans, studies demonstrate this sustained pattern of neural activity during
WM maintenance (Funahashi, Bruce, & Goldman-Rakic, 1990; Fuster & Alexander, 1971; Todd & Marois, 2004; Xu & Chun, 2006; Vogel & Machizawa, 2004; Vogel, McCollough, & Machizawa, 2005; Magen, Emmanouil, McMains, Kastner, & Treisman, 2009). These studies, however, have mainly focused on an entire stimulus array during maintenance, rather than individual items during encoding.

It has also been demonstrated that in order to encode, maintain, and retrieve a visual item, there must be communication in neural networks, rather than in a single neural population (McIntosh, Grady, Haxby, Ungerleider, & Horwitz, 1996; Gazzaley, Rissman, & D’Esposito, 2004; Fuster, Bauer, & Jervey, 1985). For example, functional imaging experiments show that brain regions involved in visual perception of an item (e.g. primary visual cortex (V1), and extrastriate areas in the dorsal and ventral visual streams) remain active during WM maintenance and retrieval (Offen, Schuppeck, & Heeger, 2009; Emrich, Riggall, LaRocque & Postle, 2013; Ester, Anderson, Serences, & Awh, 2013; Riggall & Postle, 2012; Serences, Ester, Vogel, & Awh, 2009; Harrison & Tong, 2009). Similarly, functional neuroimaging reveals that neural connectivity is enhanced in the lateral prefrontal cortex and extrastriate cortex when encoding and maintenance are successfully integrated in WM (Cohen, Sreenivasan, & D’Esposito, 2012). Intuitively, these studies suggest that to maintain and retrieve an item the item must first be successfully encoded. These studies also focus on neural activity for an entire WM array, rather than individual items during encoding. As such, the current investigation examines neural activity underlying each stimulus during encoding.

**Full Report versus Partial Report**
There are two types of reports asked of a participant from a memory array - a partial report or a full report. A partial report asks for a random sample of the observer’s memory for the memory array (e.g. items presented during encoding) (Rouder et al., 2008). A full report asks a participant to remember all items shown to them in a memory array (Adam et al., 2015). There are benefits to both partial and full reports, as both report designs ask a participant to encode all items shown in the memory array. However, since a partial report tests only a random memory sample, it is difficult to tell what items are actually encoded and maintained during each trial. Because a full report asks a participant to retrieve all items in a memory array, each trial can be analyzed by the number of items retrieved and the accuracy in regards to the temporal order that each item was retrieved (Adam, Mance, Fukada & Vogel, 2015). A partial report, however, only tells accuracy of the to-be-remembered item in a memory array and depends on multiple trials. Hence, a full report paradigm is used in the current investigation.

**Frequency Tagging Technique**

Frequency tagging provides a measure to monitor individual items during encoding. Frequency tagging describes the relationship between a stimulus that is periodically changing (e.g. between black and white) and the electrical potential the stimulus evokes (Regan, 1989). Steady-state visual evoked potentials (SSVEPs) are described as the neural amplitude that is a response to visual stimulation presented at specific frequencies (Norcia, Appelbaum, Ales, Cottereau, & Rossion, 2015). For instance, if a stimulus is flickering at five hertz, then the electroencephalogram (EEG) will produce the steady-state oscillation at that same frequency producing a ‘frequency tag’. As such, if multiple stimuli are present and are flickering at different frequencies,
the corresponding frequency tag will be modulated according to the item that is in view (Blake, 1989). Similarly, if more focused attention is given to a flickering stimulus, the corresponding frequency tag increases as compared to a stimulus that is not given focused attention (Morgan, Hansen, & Hillyard, 1996; Hillyard & Anllo, 1998; Hillyard, Muller, & Teder-Sälejärvi, 1998; Zhang, Jamison, Engel, He, & He, 2011; Muthu, Suzuki, Joon Kim, Grabowecky, & Paller, 2007). If there are multiple stimuli simultaneously shown and flickering at different rates, the frequency tags for each stimulus are shown on the EEG as long as the participant is viewing both stimuli (Zhang et al., 2011; Appelbaum, Wade, Pettet, Vildayski & Norcia, 2008).

Previous studies show that if two flickering stimuli perceptually interact with one another during WM encoding, by grouping, for example, then the frequency tags of each image will sum non-linearly (Zhang et al., 2011; Appelbaum et al., 2008). For example, if a participant is allocating their attention to a stimulus that is flickering at 5 Hz and a stimulus that is flickering at 3 Hz, these stimuli will sum non-linearly to 8 Hz. Thus, if a frequency tag sums non-linearly, individual items presented during WM encoding can be monitored on the EEG.

Frequency tagging allows attentional processes and WM encoding processes to be studied with greater detail than in previous experimental paradigms because frequency tagging provides a cohesive measure of how attention is being allocated to individual items in a memory array. As stated above, if more attention is allocated to a stimulus, the resulting frequency tag will be higher than if less attention is given to a stimulus (Morgan, Hansen, & Hillyard, 1996; Hillyard & Anllo, 1998; Hillyard, Muller, & Teder-Sälejärvi, 1998; Zhang, Jamison, Engel, He, & He, 2011; Muthu, Suzuki, Joon Kim,
Grabowecky, & Paller, 2007). As such, frequency tagging can be used to assess how large the frequency tag amplitude is for each item in a memory array. A previous study from this lab used frequency tagging with a partial report paradigm (e.g. recognition WM paradigm) and found that frequency tags for all items shown in the memory array were greater on to-be-probed items in correct trials as compared to to-be-probed items in incorrect trials (Peterson, Gurariy, Dimotsantos, Arciniega, Berryhill & Caplovitz, 2014). These results are consistent with the ‘all or nothing’ model (Rouder et al., 2008).

However, another question can be asked regarding other items in the array: are the frequency tags for these other items also higher on correct trials? If the frequency tags for the other items of the memory array are also higher on correct trials, this outcome suggests that attentional resources were available across the entire stimulus array, which is consistent with the ‘all or nothing’ attentional model. However, if only a subset of the items in the memory array shows increased frequency tags, this outcome would indicate that attentional resources were only given to a subset of stimuli, which is consistent with the ‘graded attentional’ model. It is important to remember, that salient attention has to be given to a stimulus. Otherwise, that stimulus will not be encoded. Hence, frequency tagging allows an individual to examine what items were given attention and compare these items to what items were actually retrieved. Figure 2 is a visual display of the attentional models and expected frequency tags.
Figure 2. Attention models and expected normalized amplitudes. This figure provides a visual representation of how attention is allocated as a memory array is shown. (1) In the ‘graded attention’ model, attentional resources are allocated to a specific subset of items (e.g., blue and yellow). Hence, the frequency tags are expected to be higher for items attended to as compared to unattended items. (2a) The ‘all or nothing’ model is explained through full attention or attentional lapses. When all items are attended to in a memory array, it is expected that the frequency tags for all items will relatively high. (2b) However, when an attentional lapse occurs, frequency tags will be decreased for all items. This model is derived from Peterson et al., 2014.
**Approach & Aims**

This thesis investigated two models of attention: the ‘graded attention’ model and the ‘all or nothing’ model by using the frequency-tagging technique to examine items presented at the encoding phase of a WM full report paradigm. In this full report paradigm, participants encoded four items and then recalled all items presented at retrieval. The frequency tagging technique paired with the full report paradigm (a novel paradigm) allowed items that were actually attended to, to be tagged according to the frequency at which they were flickering. In regards to the ‘all or nothing’ model, cognitive resources are allocated to all items unless an attentional lapse occurs. Hence, in the ‘all or nothing’ model, frequency tags should appear greater for all items if the items are correctly attended to. However, if all four items were not retrieved correctly, this incorrect retrieval would demonstrate that WM failed during the maintenance stage.

The ‘graded attention’ model states that a subject will attend to a subset of the items shown. If the data support the ‘graded attention’ model, then frequency tags should only appear on the EEG for the items that were actually attended to. If this subset of items was not retrieved correctly, this incorrect retrieval would show a failure in WM maintenance. In the current investigation, unique frequencies were assigned to items presented during encoding: 3 Hz, 5 Hz, 12 Hz, 20 Hz. These unique frequencies allowed each encoded stimulus to be ‘tagged’ according to the frequency in which the stimulus was flickering. Upon retrieval, items were sorted upon whether the item was correctly retrieved or incorrectly retrieved (forgotten). The SSVEP amplitude were then calculated for correctly retrieved items and forgotten items.
A previous study from this laboratory used the frequency tagging technique with a partial report paradigm to study neural amplitudes of items in a memory array (Peterson et al., 2014). Peterson et al. (2014) found that SSVEP amplitudes during encoding were observed to be significantly higher for items correctly remembered as compared to items that were later forgotten. These results were consistent with the ‘all or nothing’ model. As such, in extending this previous work we expected similar results in regards to the SSVEP amplitudes of correctly retrieved items. The full report paradigm, however, provides more information about the fate of all items presented during encoding. Instead of employing a partial recall task, the full report asked for full recall of items presented. The full report allowed for comparison between items that were encoded to items that were actually retrieved. For example, even though three items may have been encoded (based on the frequency tags of each item), a participant may only successfully retrieve two of those items, reflecting a failure in maintenance or retrieval.

Overall, the goal of the current research is to understand the neural processes underlying encoding. Previous research studies, as shown above, have been limited to studying an entire stimulus array during maintenance. This thesis, however, disentangles how each stimulus is encoded with the frequency tagging technique to further understand the stages of WM. This research aims to inform the ‘graded attention’ and the ‘all or nothing’ attentional models.
Methods

Participants

Twenty-six adults participated in this study (13 males, 19-35 years of age). Six datasets (6 participants) were excluded from the 26 datasets because the electroencephalogram (EEG) data were unusable (e.g. too many eye movements and/or eye blinks). Participants were instructed to fill out a demographics form for the Internal Review Board. Each demographics sheet asked about the participants age, gender, handedness and what ethnicity they most closely identified with. Participants were also asked about their vision. If a participant wore glasses, he/she was allowed to wear his/her glasses over the EEG electrodes. Participants were not allowed to participate in the study if they were unable to see the shapes clearly. Out of the usable participant data (N=20), eighteen participants were right-handed and two participants were left-handed. All participants had normal to corrected-to-normal vision and were in good health with no history of neurological disorders. The Institutional Review Board at the University of Nevada, Reno approved all experimental protocols. Each participant gave written, informed consent prior to participating in the experiment according to the guideline of the University of Nevada Reno Internal Review board. For a visualization of the age, gender and handedness of each participant, see Table 1 in the Appendix.

Stimulus Apparatus & Display

Stimuli were presented on a Mitsubishi Diamond Pro270 (20in, 1024x768, 120Hz). The stimulus computer is a 2.6 GHz Intel Core i7 (4GB 1600 MHz DDR3 RAM) Mac Mini with an Intel High Definition (HD) 4000 graphics processor (768MB of DDR3 SDRAM). Stimuli were created with Adobe Illustrator (Adobe Systems Inc, San
Jose, CA) and presented with the Psychophysics Toolbox version 6.1 (Brainard, 1997; Pelli, 1997) for MATLAB version R2012b (Mathworks Inc., Natick, MA). The colors of the stimuli are black (0.1538 cd/m²) and white (76.49 cd/m²) and were positioned on a uniform gray background (15.63 cd/m²).

Electrophysiological Apparatus & Recordings

The EEG data were collected using a Geodesic high-density EEG System (HD-EEG) 300 with a HydroCel Geodesic Sensor Nets (GSN) 130, 256-electrode cap at a sampling rate of 1000 Hz. The HD-EEG was amplified using an EGI Net Amps Bio Amplifier with a gain factor of 20 K per channel and digitized using a Texas Instruments analog to digital converter (ADS 1251, 24 bit, 20 KHz). The data were then recorded using the Net Station 5.0 software package (Electrical Geodesics, Inc., Eugene, OR, USA). Electrical impedances for the majority of the electrodes were kept below 50 Ω. Prior to data collection, a photodiode was attached to the cathode ray tube (CRT) monitor and was used to temporally synchronize the stimulus presentation onset with the recorded EEG to ensure the accuracy of timing. Photodiode output was amplified using a transimpedance amplifier and digitized with the EEG data via one channel of the analog-to-digital (AD) converter.

Task Design & Procedure

Participants performed a visual working memory (VWM) full report paradigm with a set size of four items. Each trial started with a blank fixation screen, presented for 600 ms plus or minus random jitter between 0 and 100 ms, with a central fixation point approximately 0.3° x 0.3° (degrees of visual angle) and four black squares, approximately
1.2º x 1.2º. The black squares were placed to denote the location of the four stimuli and to prevent any contamination from visual onset evoked potentials.

During encoding, test stimuli were presented (1000 ms) at the center of the four quadrants of the screen plus random jitter between -1.5º and 1.5º. Test stimuli were chosen randomly from 10 polygons generated in Adobe Illustrator (Figure 3).

![Figure 3. Stimuli shown during experiment. Four out of these ten stimuli were pseudorandomly assigned to a location to be presented at each encoding phase of each trial of the experiment.](image)

Each polygon flickered at one of four possible frequencies (3 Hz, 5 Hz, 12 Hz, and 20 Hz) each of which was pseudorandomly assigned to a location. These frequencies were chosen because the encoding duration (1000 ms) permitted exact periods of stimulation using a 120 Hz frame refresh rate. Another reason why these frequencies were chosen was because the harmonics of each fundamental frequency are independent of one another, which allowed the fundamental frequency of each stimulus to be recorded, as well as the second and third harmonic. Following the presentation of the stimuli, a blank screen was presented (1000 ms). During retrieval, all 10 possible polygons were placed in the center row of the screen, as shown in Figure 4. Retrieval demands included two types of testing: simultaneous recall and sequential recall. During
Simultaneous recall, participants dragged polygons into one of the four possible quadrants in an order of their choice with a computer mouse. In the sequential recall, participants were forced to place each stimulus in a randomly designated quadrant during testing. Sequential recall was included to prevent any potential strategies due to grouping only a subset of the encoded items. Responses were untimed for both the simultaneous and sequential recall types. Each recall type (simultaneous and sequential) was randomly presented in 3 blocks with 25 trials each. In total, each recall type was presented 75 times resulting in a total of 150 trials per experiment. See Figure 4 for a visual representation of the paradigm.
1. Fixation

2. Encoding

3. Maintenance

4a. Sequential Recall

4b. Simultaneous Recall

Figure 4. Visual working memory task design. This figure represents the trial sequence for the full-report paradigm tested. (1) During fixation, four black squares were presented in each quadrant for 600 ms. (2) Fixation was followed by encoding for 1000 ms. During encoding, each stimulus flickered at a unique frequency (3 Hz, 5 Hz, 12 Hz, and 20 Hz) in each of the four quadrants of the screen. Participants were instructed to remember the location of each of the four items shown during encoding. (3) Following encoding, a maintenance delay period occurred for 1000 ms. (4) Finally, there were two testing types. (4a) During *sequential* recall, participants were randomly designated a location to place each polygon. (4b) During *simultaneous* recall, participants were instructed to place the four encoded polygons in an order of their choice.

Before the task, each participant was instructed to decrease the movements he/she made during the experiment. Specifically, each participant was asked not to blink, move his/her jaw, or move his/her eyes away from the central fixation cross (located in the center point of the computer screen) during the ‘encoding’ period. Each participant was shown how these movements affected the EEG trace before participating in the experiment. Each participant was told that when he/she did need to blink, that he/she
could do so during retrieval, as I was solely interested in the EEG trace created during the 1000ms encoding period. For the task itself, subjects were instructed to remember the quadrant that each polygon was presented at during encoding. Each participant was instructed that he/she would have two recall tasks during the experiment. During the simultaneous task, a participant placed each shape in the quadrant order of his/her choice. During the sequential ask, the computer would assign the order that each quadrant was tested. I asked each participant if he/she had any additional questions after I gave him/her instructions. Before starting the experiment, participants completed ~5 practice trials with each recall type to familiarize themselves with the task.

**Behavioral Data Analysis**

Behavioral accuracy was calculated for simultaneous and sequential recall for each participant. The behavioral accuracy for each participant was averaged across all of the usable participants (i.e. N=20) to find the total accuracy. Accuracy was calculated as a percentage of correct trials (hits and correct rejects) out of all trials presented for each recall type. Accuracy was also calculated for the order of items retrieved. For example, if a participant correctly placed the first item of the memory array but incorrectly placed the second item, his/her accuracy was 100% for the first item and 0% for the second item. The percentage of trials in which a participant correctly recalled 0 items, 1 item, 2 items, 3 items, or 4 items was also calculated. Participants correctly recalled anywhere from 0 items to all 4 items (presented in the memory array) out of the 75 trials in each simultaneous and sequential recall. See the ‘Results’ section to view behavioral data.
Electrophysiological Data Analysis

The EEG data were processed and analyzed using a combination of functions from the Net Station software package, Brainstorm software package (Tadel et al. 2011: http://neuroimage.usc.edu/brainstorm), and custom-made Matlab scripts. Data from correct and incorrect trials were analyzed. First, in Net Station, the data were high pass filtered (> 0.5 Hz) and cleaned for artifacts (e.g. eye movements, eye blinks, and bad channel detection). The data were then segmented into 1000 ms epochs (150 total epochs). Each recall type (simultaneous and sequential) consisted of 75 epochs apiece.

The custom-made Matlab scripts were able to sort individual trials by recall type (simultaneous or sequential), accuracy, and frequency (3 Hz-correct, 3 Hz-incorrect, 5 Hz-correct, 5 Hz-incorrect, 12 Hz-correct, 12 Hz-incorrect, 20 Hz-correct, 20 Hz-incorrect). When comparing correct and incorrect items (i.e. polygons) for each frequency, the number of items that were correct and incorrect must be the same (e.g. the number of items for correct or incorrect must never exceed the other). For example, if there were 30 correct items and 20 incorrect items for 3 Hz, 20 correct items would be pseudorandomly selected (by the custom-made Matlab scripts) to match the number of incorrect items. After matching the number of correct and incorrect items, the correct and incorrect items were each averaged. For each electrode, a fast Fourier transform (FFT) was applied to the average correct items and the average incorrect items to extract the SSVEP amplitude of the fundamental (3 Hz, 5 Hz, 12 Hz, 20 Hz) and secondary (6 Hz, 10 Hz, 24 Hz, 40 Hz) harmonic corresponding to each item encoded in the memory array. Both the primary and secondary harmonics were used to create the difference index, described below. The process of matching the number of correct and incorrect items,
averaging correct and incorrect items, and applying the FFT was performed 10,000 times using different pseudorandomly chosen correct and incorrect items.

In order to control for confounding attentional effects caused by using a range of frequencies, index values were calculated for each electrode which allowed for the data to be averaged across frequencies (i.e. difference indices). Difference indices act as a standardized measure of SSVEP amplitude that compared correct and incorrect items independent of frequency. Difference indices were calculated using Formula 1:

\[
\text{Formula 1. } \text{Index}_F = \frac{(F_{\text{correct recall}} - F_{\text{incorrect recall}})}{(F_{\text{correct recall}} + F_{\text{incorrect recall}})},
\]

where \( F \) corresponds to the amplitude of a given frequency (fundamental or secondary frequency for each item in the stimulus array).

Index values were calculated using the difference between amplitudes for an item when that item was recalled correctly versus when it was not recalled correctly. A positive index value indicates that amplitudes were greater for correctly recalled items, whereas negative index values represent greater amplitudes for incorrectly recalled items (i.e. forgotten items). An index value of zero means there is no difference between the amplitudes of correct and incorrect trials. See Figure 5 for a visual representation of the data analysis.
We were interested in how indices differed across different regions of the brain when an item was remembered versus later forgotten. Specifically, we were interested in how indices differed in the frontal cortex, parietal cortex, and occipital cortex. To assess how these brain regions differed in their responses, we clustered EEG electrodes based upon each electrode’s location on the skull. Electrodes found above the frontal lobes were clustered into the ‘frontal’ group, electrodes found above the parietal lobes were clustered...
into the ‘parietal’ group, and electrodes found above the occipital lobes were clustered into the ‘occipital’ group. The electrodes that were chosen to be in the ‘frontal’, ‘parietal’, and ‘occipital’ clusters were kept constant across all participants. The index values for the simultaneous and sequential trials were averaged within each electrode cluster. Here, we reference the location of our electrode placement, as electrode placement will be useful when viewing the differences in amplitudes in the frontal, parietal, and occipital cortices. For a visualization of how electrodes were clustered, see Figure 6.

Figure 6. Electrode cluster selection. Electrodes were chosen based upon the locations of the frontal, parietal, and occipital lobes. We clustered electrodes because we were interested in how each of these brain regions individually responded to remembering versus forgetting an item. These regions will be useful in the results sections where we compare index values of the frontal, parietal, and occipital cortices.
Results

Behavioral accuracy

Behavioral performance for the WM task was first examined. To see if percent accuracy differed between the simultaneous and sequential tasks, we conducted a paired t-test. This t-test showed that performance for the tasks was significantly different: \( t(19)=5.058, p=0.00007 \) (Simultaneous \( M = 56.74\% \ (2.70); \) Sequential \( M = 47.49\% \ (3.02) \)). This t-test showed that the simultaneous task was easier than the sequential task which makes sense because participants were allowed to place items in an order of their choice during the simultaneous task but not the sequential task. We note that chance performance in these tasks is difficult to calculate because we used a full report paradigm. Recognition paradigms have chance performance of around 50%, whereas this task’s chance performance was 10% for the first item and even smaller for subsequent items placed. For individual participant accuracy, see Table 2 in the appendix. For a visual representation of behavioral accuracy, see Figure 7.
Percent accuracy for response order was calculated to assess how difficult it was for participants to place each item during the recall tasks. In *simultaneous* recall, participants retrieved the first item with 87.65% (SD = 1.76) accuracy, the second item with 72.35% (SD = 2.82) accuracy, the third item with 44.21% (SD = 4.70) accuracy, and the fourth item with 22.74% (SD = 3.05) accuracy. In the *sequential* recall, participants retrieved the first item with 62.95% (SD = 3.21) accuracy, the second item with 45.82% (SD = 0.96) accuracy, the third item with 41.96% (SD = 3.50) accuracy, and the fourth item with 40.42% (SD = 3.56) accuracy. It can be seen in the *simultaneous* task that percent accuracy was higher than sequential recall for the first, second, and third items. However, for the fourth item placed, *sequential* recall had a higher percent accuracy. These results make sense, as in the *simultaneous* task, participants were able to place items in the order they remembered the items. However, in the *sequential* task, participants were assigned order. Because participants were assigned order in the
sequential task, there were likely trials in which a participant remembered the fourth item better than the first item. See Figure 8 for a visual representation of response order accuracy.

![Figure 8. Response order accuracy. Plotted is behavioral performance (% correct) for response order in the simultaneous and sequential recall types. It can be seen that the first item placed had the highest accuracy and the fourth item placed had the lowest accuracy throughout both simultaneous and sequential recall types. Sequential recall had lower accuracy than simultaneous recall on all items except for the fourth item placed. Error bars represent standard error of the mean.](image)

The percentage of trials in which a participant correctly recalled 0 items, 1 item, 2 items, 3 items, or 4 items was also calculated to evaluate how many items participants were actually able to remember trial-by-trial. In the simultaneous recall task, participants retrieved 0 items in 4.77% of the trials, 1 item in 17.44% of the trials, 2 items in 36.77% trials, 3 items in 27.81% of the trials, and all 4 items in 13.02% of the trials. In 77.6% of the trials, participants remembered 2, 3, or 4 items during simultaneous recall. In the sequential recall task, participants retrieved 0 items in 13.44% of the trials, 1 item in
22.95% of the trials, 2 items in 30.12% trials, 3 items in 22.25% of the trials, and all 4 items in 9.44% of the trials. In 61.81% of the sequential trials, participants were able to retrieve 2, 3, or 4 items. Overall, in the majority of trials, participants remembered two items and forgot two items. There were only a subset trials where participants remembered all four items or when participants forgot all four items. See Figure 9 to see a visual of the percent of trials with x items recalled.

![Figure 9](image)

Figure 9. Percentage of trials with x items recalled. Plotted is the percentage of trials where x items were recalled (x = 0 to 4). In most trials, participants recalled 1, 2, or 3 items. Error bars represent standard error of the mean.

**Frequency Tag Amplitude During WM Encoding**

For frontal, parietal, and occipital electrodes, index values were averaged across frequencies for *simultaneous* and *sequential* recall. Index values are calculated using the difference between amplitudes of an item when it is correctly recalled (positive index value) versus not correctly recalled (negative index value). An index value of zero means there is no difference between the correct item’s amplitude and the incorrect item’s amplitude. As such, the index value for each set of electrodes was compared to zero with
a one-sample t-test. For frontal electrodes, the index value for sequential recall was significantly higher than zero: \( t(19)=2.55, p=0.020 \) (Index value \( M = 0.0567 \) (0.0057)).

Simultaneous recall approached significance: \( t(19)= 1.88, p= 0.0755 \) (Index value \( M = 0.0868 \) (0.0031)). In the parietal electrodes, the index values for both simultaneous recall \( t(19)=2.98, p=0.008 \) (Index value \( M = 0.0846 \) (0.0036)) and sequential recall \( t(19)=2.76, p=0.013 \) (Index value \( M = 0.0677 \) (0.005)) were significantly greater than zero. Index values for simultaneous recall \( t(19)=3.50, p=0.003 \) (Index value \( M = 0.1038 \) (0.0049)) and sequential recall \( t(19)=3.40, p=0.003 \) (Index value \( M = 0.0853 \) (0.0054)) were significantly greater than zero in occipital electrodes as well. Overall, the electrode sites showed that SSVEP amplitudes were greater for correctly remembered items than for forgotten items. For a visualization of individual index values, see Table 3 in the Appendix.

I conducted an analysis of variance (ANOVA) to see if there were any main effects of task or electrode site. This 2 task x 3 electrode repeated measures ANOVA revealed no statistically significant main effects of task or site with all \( p \) values greater than 0.26. This analysis indicates that all of the index values for the frontal, parietal, and occipital electrodes were similar to one another in magnitude across electrodes and tasks. See Figure 10 for a visualization of how the index values were similar to one another.
Figure 10. Average index values for each electrode cluster and condition. The graph shown represents average index values for each electrode site in simultaneous recall. The second graph shows average index values for each electrode site in sequential recall. Error bars indicate standard error of the mean. Electrode location is also shown to provide a visual of where the frontal, parietal, and occipital cortices are located.

Topographic maps were created to show how amplitudes differed for correct versus incorrect retrieval across all electrodes on the scalp. These topographic maps allowed us to visualize how neural activity in the brain during encoding differed for correct trials as compared to incorrect trials. See Figure 11 for this visualization.
Figure 11. Topographic maps for sequential and simultaneous recall. Topographic maps represent index values for simultaneous and sequential conditions. Positive index values represent higher amplitudes when an object was correctly recalled and negative index values represent higher amplitudes when an object was incorrectly recalled. The scale represents an index value of -0.2 (blue) to 0.2 (red).
Discussion

Current Investigation & Goals

In the current investigation, we investigated the encoding stage of WM using a novel full report design paired with the frequency-tagging technique. During encoding, each stimulus flickered at a unique frequency, which allowed analysis of neural activity in response to each item during WM encoding. As every item from each WM array was probed during WM recall, it was possible to assess the frequency tag amplitudes for correctly recalled items and later forgotten items. Overall, it was shown that frequency tag amplitudes during encoding were significantly higher for items correctly retrieved as compared to those later forgotten items. These results confirm a previous study from this lab that also found that frequency tag amplitudes were higher for correctly retrieved items as compared to later forgotten items (Peterson et al., 2014). As the frequency tag amplitudes were modulated during WM encoding, these data confirm that encoding plays a large role in capacity limitations. These data also clarify that encoding related operations engage wide swaths of cortex including occipital, parietal and frontal regions. The ANOVA conducted revealed that frequency tag amplitudes were not significantly different in each electrode site (frontal, parietal, and occipital) nor in task type (simultaneous and sequential). These data indicate that participants have similar neural responses across the whole brain in response to encoding a stimulus into WM.

One of the goals of the current investigation was to test two different attentional models. The first model, the ‘all or nothing’ model describes that a participant will either remember all items from a WM array or forget all items, as a result of an attentional lapse. The second model, the ‘graded attention’ model states that attention is graded
depending on a WM capacity. The ‘all or nothing’ model suggests that attention is allocated to all items during encoding, whereas the ‘graded attention model’ describes that attention can be allocated to a subset of items during encoding. The current data support the ‘all or none’ model, as SSVEP amplitudes were significantly greater for correct items than incorrect items. Because amplitudes were greater for correct items, these data indicate that participants attempted to allocate attention to all items shown to them. These data are consistent with behavioral measures by Mance, Adam, Fukada & Vogel (2014), who conducted a full report experiment and designated a ‘lapse’ trial as only retrieving 1 item or less. Mance et al., (2014) found low WM and high WM capacity participants to have average ‘lapses’ of 12.1% and 7.4%, respectively. In the current study, participants had 22.4% lapse trials for simultaneous recall and 38.19% for sequential recall. However, in order to fully test this model, future experiments would need to employ an experimental paradigm that has WM arrays with more than four items and probe a subset of those items for recall, as done by Adam et al. (2015). Such a paradigm allows us to overload WM on each trial, yet still probe a subset of items to see the accuracy in which these items were encoded.

Another way to assess which attentional model is more consistent with our data would be to separate participants into two groups: high WM capacity individuals and low WM capacity individuals. We could then evaluate how attentional resources were allocated for each group. If low WM capacity individuals attended to a lower subset of items than high WM capacity individuals, their results would be consistent with the ‘graded attention’ model. However, if both these groups still had entire ‘lapses’ of attention, their results would be consistent with the ‘all or nothing’ model.
Implications

Logically, without attention to an item during WM encoding, the item cannot be successfully encoded. Hence, we can infer that some neurons are responding because attention is being allocated to an item. Previous studies have shown that attention can modulate frequency tag amplitudes (Morgan, Hansen, & Hillyard, 1996; Hillyard & Anllo, 1998; Hillyard, Muller, & Teder-Sälejärvi, 1998; Zhang, Jamison, Engel, He, & He, 2011; Muthu, Suzuki, Joon Kim, Grabowecky, & Paller, 2007). These studies suggest that frequency tag signals can predict when more attention is allocated to a stimulus array. To measure the allocation of attentional resources, future experiments could include a distractor flickering amongst an array of items to-be-encoded. The SSVEP waveform corresponding to the distractor on correct and incorrect trials would be an indicator of how much attention was given to the items to-be-encoded and the distractor.

Overall, through examination of SSVEPs, it can be inferred that a participant will attempt to encode all items shown in a memory array, as is consistent with the ‘all or nothing’ attentional model. Attention plays a large role in the SSVEP waveform formed as a result of encoding these items. If attention fails during the encoding process, items will more likely be forgotten. As such, attention and encoding are very important to consider when studying WM.

A metaphor presented in the introduction involved remembering the digits of a phone number, where encoding was presented as the initial perception of a phone number entering the brain. We were able to detect the encoding process with frequency tags to see items (e.g. digits) remembered and items (e.g. digits) forgotten. Our results highlight
the importance of attention in WM. Without attention to a phone number, an individual cannot recruit the neural resources to remember that phone number later.
References


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doi:10.1016/j.neuropsychologia.2011.02.017


Appendix

Table 1. Participant demographics. This table shows participant demographics. A total of 26 subjects participated in this experiment (13 males and 13 females). Six out of these 26 datasets were thrown out due to excessive eye movements during the EEG recording. Out of the usable traces, there were 8 males and 12 females that participated. Race is not included in this table to maintain participant privacy.

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Table 2. Individual Participant Accuracy. This table shows percent accuracy for individual participants for the simultaneous and sequential trial types. Accuracy was calculated as a percentage of correct trials out of all trials presented for each recall type.

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Table 3. Index values for individual participants. Table 1 shows index values for individual participants. Each participant completed the sequential and simultaneous tasks, where index values were created for the frontal, parietal, and occipital regions.

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