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Decoding the contents of working memory using EEG provides evidence for the sensory recruitment hypothesis

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By

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Recent fMRI studies have shown that the contents of visual working memory can be decoded from early visual areas, including V1. This result has been interpreted as support for the sensory recruitment hypothesis: the idea that the neurons responsible for vision also sub-serve visual working memory and visual imagery. However, whereas these results imply that the same brain areas are responsible for vision and visual memory, they do not rule out the possibility that these processes rely on completely different populations of neurons within these areas. For example, although viewing and remembering an orientation might lead to the same global radial bias pattern in V1, entirely different neurons may produce these patterns during vision and memory. We develop a novel EEG paradigm that allows us to directly test whether the same neurons responsible for processing incoming visual signals are indeed modulated by an internally driven memory signal. Participants held an orientation in working memory while viewing a flicking visual noise patch. This flickering stimulus generated an EEG response known as the steady state visually evoked potential (SSVEP), a measure of early neural responses to the noise stimulus. Critically, if memory

relies on these same visual neurons, then the SSVEP response to visual stimulation should also carry information about the stimulus being held in memory. We confirm this prediction by showing that a multivariate pattern classifier can be used to identify a remembered orientation from the stimulus-driven SSVEP. This finding demonstrates a direct interaction between a bottom-up stimulus-driven signal and a top-down memory-driven signal, providing strong evidence for the sensory recruitment hypothesis and a powerful new approach for investigating visual memory with EEG.

Key words: sensory recruitment hypothesis, visual working memory, SSVEP

CHAPTER 1

INTRODUCTION

Humans have the ability to imagine colors, faces, objects, or even visualize a map to remember which road to take. We can create and envision images in our mind without any outside influence. In this very moment, you can close your eyes and imagine a tiger and "see" it in your mind. In this scenario, you are using prior information from memory (what tigers look like) and bringing it to your focus of attention. Visual information that is held in mind in this manner is thought to be stored in *visual working memory* (VWM; Luck & Vogel, 1997; Zhang & Luck, 2008). This memory system allows us to call forth information and utilize it in our everyday lives. With this incredible ability, the question of interest emerges of how we are able to do this.

Holding an image of a tiger in mind is not exactly the same mental phenomenon as actually seeing a tiger. For example, when you imagined a tiger, you could see that it has four legs, fur, and stripes, but most people are not able to report how many stripes their imaginary tiger had, whereas a person looking at a tiger would be able to easily count the number of stripes. Nonetheless, the act of picturing visual images has similarities to actually seeing it, and psychologists have long hypothesized that the same brain processes involved in visual perception may play a role in visual memory. In particular, the *sensory*

recruitment hypothesis (SRH) posits that the same neurons responsible for processing incoming visual information are also used to represent visual information stored in VWM (Pasternak & Greenlee, 2005; Kosslyn, Ganis & Thompson, 2001). For example, the brain has cells that process the color red. The sensory recruitment hypothesis predicts that these same cells are responsible for the ability to retain the same shade of red in memory.

The sensory recruitment hypothesis makes many predictions about how the brain should act when information is maintained in visual memory. One of the most distinct predictions asserts that the same areas of the brain should be active when looking at an image and visualizing the same image. If the brain is recycling the same neurons to both see and remember images, then that area must be active for both scenarios. As detailed below, a great deal of support for this prediction has recently been found using functional magnetic resonance imaging (fMRI) to study human brain activity during vision and visual memory (Harrison & Tong, 2009; Serences, Ester, Vogel, & Awh, 2009; Pratte & Tong, 2014). Despite fMRI being able to show that the same overall brain areas play a role in both vision and visual memory, this brain recording technique is only able to measure relatively large chunks of brain, rather than individual neurons. This approach is therefore not able to test what we labeled as the "strong" sensory recruitment hypothesis: the assertion that the individual neurons are the same for both vision and visual memory. In this thesis, a new experimental approach that utilizes electroencephalogram (EEG) to measure brain activity is developed providing a way to test the strong hypothesis. The results suggest that the neural system supports the strong hypothesis, but a brief overview of vision and visual memory will be given first for further understanding.

1.1 Neural Basis of Vision

Neurons in the brain are spatially grouped by the specific functions they perform. For example, vision is localized in the occipital lobe at the back of the brain (see Figure 1.1). The neurons within this system are specialized for the process of responding to light waves and building meaningful representations from this sensation. Specific brain regions also exist for many other sensory functions, such as auditory processing and sense of touch.

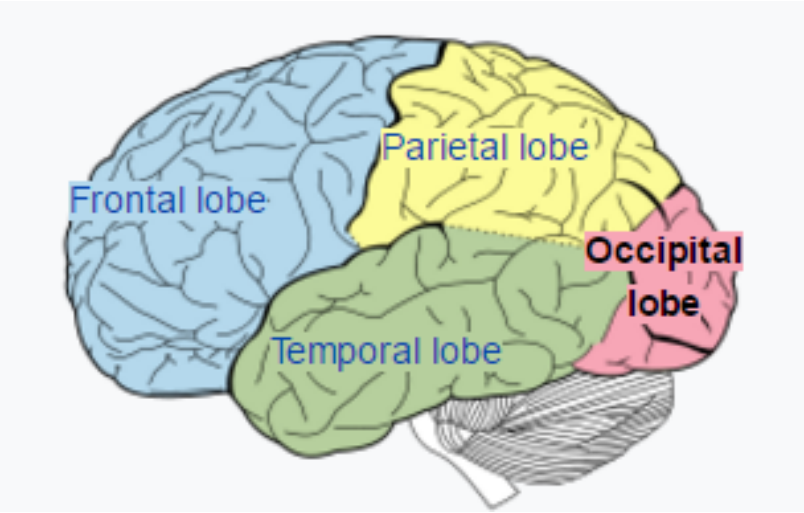

Figure 1.1: Main sections of the brain. Original by Henry Gray, 1918, digitally retouched via Wikimedia Commons. Used under Creative Commons Attribution 2.0 Generic.

When the brain receives incoming sensory information from the eyes, the neurons that exist in these specialized regions work to process this information. For example, there are neurons in the early visual cortex (V1) that respond to a specific location in space, a particular line orientation, or a certain color (Hubel & Wiesel, 1968). The activity of sensory neurons in response to incoming sensory information is known as *bottom-up processing*,

such that information is processed starting with the basic sensation (e.g. light on the eye) and works up to more complex forms of information (e.g. understanding where an object lies in the visual field).

However, not all functions of the brain are localized, and not all processes are bottom-up in nature. Attention, for example, does have some specialized brain regions (e.g. the parietal lobe; Todd & Marois, 2004), but attention also influences other functions such as vision and hearing, therefore acting throughout the brain. Attention is used throughout daily life to select only a portion of incoming information for processing, such as when someone shifts their gaze to a car stopping in front of them or when they tune out the conversations surrounding them at a party. In these scenarios, attention is altering how the brain processes incoming sensory information via *top-down processing*.

Top-down processes are often thought to be governed by the internal, higher level processing in the brain typically associated with the prefrontal cortex (see Figure 1.1). For example, when a person chooses to attend to visual stimulation, higher-level processes ("top") act on lower-level visual processes ("bottom") to facilitate processing of that specific information at the expense of other incoming sensations. Visual attention demonstrates that higher level processes can influence and work in tandem with the lower order processes, such as early visual areas. The sensory recruitment hypothesis then goes a step farther predicting purely top-down processing can activate early visual areas in the absence of bottom-up stimulation.

1.2 Neural Basis of VWM

Reactivation of sensory neurons independent from the environment may seem like science-fiction, but just moments ago, this reactivation was possible when imagining a tiger. Imagining a tiger involves VWM, in that the image of a tiger is pulled from long term memory and put into VWM where it is now visible or at the focus of attention. These ideas of "visual imagination" and "visual working memory" are often thought to be the same process (Tong, 2013). Both processes require allocating attention to memories and retaining information in mind, therefore both will be referred to as VWM in this paper.

To study the capabilities of visual working memory, experimental tests must use more controlled tasks than the imagining of a tiger. In laboratory tests of VWM, a stimulus (e.g a colored square) is shown to a person and then taken away. After some brief delay interval (around 1 second) the person is tested on their knowledge of this stimulus by asking whether it was red or green. This example experiment is a test of visual working memory because the participant must store the color in mind without any visual input, for a brief period, to correctly answer questions about the color. Despite the fact that this memory system is typically testing retention of information for only a few seconds, research has shown the memory system to be a highly accurate way to store visual information for a period of over 30 seconds (Magnussen & Greenlee, 1999). In addition to a limited duration, this working memory is also severely limited in how much information it can hold, typically thought to be only a few items (e.g. colors or shapes) at any given time (Luck & Vogel, 1998; Miller, 1956; Zhang & Luck, 2008).

Researchers have sought to understand how the brain works to store these visual working memories. For many years, memory was believed to be localized such that a place in the brain existed where all memories were stored. Much work identified areas in the parietal lobe (see Figure 1.1) as being critical for working memory (Todd & Marois, 2004). However, visual information is able to be held in great detail in visual working memory, such as a particular line orientation or particular shade of red. Because cells capable of representing this visual information with such detail do not exist in the parietal lobe, researchers continued to believe other areas, such as early visual areas, play a role in VWM.

As previously stated, neurons in the visual cortex are tuned to prefer a certain orientation, location, or color. During visual stimulation, details about the viewed stimulus are present in the neural activity of V1. If the sensory recruitment hypothesis is true, details about a remembered stimulus should also be present in the neural activity of V1. This leads to a strong prediction of the sensory recruitment hypothesis: If researchers could probe the brain to see what information is contained in a particular neural activity pattern, then V1 should contain information about whatever stimulus is being remembered, even if there is no visual stimulation.

More recent research on VWM in humans has provided strong support for the idea that early visual areas contain information about the contents of memory. In their seminal study, Harrison and Tong (2009) measured human brain activity with fMRI and combined this measurement with a "mind-reading" technique to determine whether information held in memory was supported by these brain areas. This "mind-reading" technique used machine learning to backwards solve the contents of VWM from the fMRI data alone. In their

study, two oriented sine wave gratings (see Figure 1.2) were shown one after another. Following these stimuli, participants were cued with a "1" or "2" indicating which of the two orientations to remember. Subjects then focused on maintaining this memory over a 12 second retention period. During this retention period, the researchers attempted to figure out what orientation the subjects were holding in mind based solely from the measured brain activity patterns in early visual areas. Their success in this "mind-reading" provides tremendous implications for VWM. The activity patterns were in early visual areas, suggesting that these brain regions carry information about the contents of visual memory, therefore supporting the sensory recruitment hypothesis.

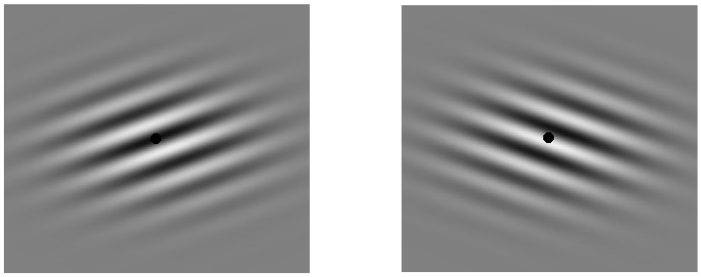

Figure 1.2: Sine wave gratings

1.3 The "Strong" Sensory Recruitment Hypothesis

The fMRI work of Harrison and Tong and many subsequent demonstrations (Serences, Ester, Vogel, & Awh, 2009; Pratte & Tong, 2014) strongly suggests that early visual areas play a critical role in both vision and VWM, but due to the coarse resolution of fMRI (e.g. 3mm chunks) research has yet to determine whether the same neurons are involved in the

same process. For example, two systems of neurons, one for response to external stimuli and one for activation from internal memory processes, could exist in parallel, physically located right next to each other. This arrangement would explain the results found with fMRI but does not provide evidence for the "strong" sensory recruitment hypothesis. In fact, this parallel system could very well be possible, given what is known about early visual areas. For example, Figure 1.3 shows the earliest visual area V1, which is made up of distinct layers. The fourth layer is known to receive bottom-up information from the eyes, while the other layers largely receive top-down information that is fed back from higher-level brain areas (Lamme, Super, & Spekreijse, 1998). Therefore, layer 4 might respond to bottom-up stimulation, while another layer would respond to top-down. In this scenario, the same neurons would not be activated by vision and visual memory.

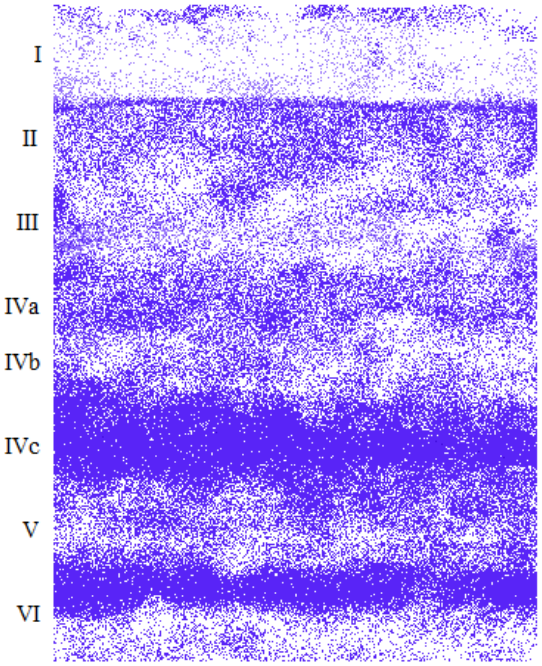

Figure 1.3: Cross section of the layers of V1

The goal of this thesis is to determine whether the strong version of the sensory recruitment hypothesis holds. No measure of human brain activity is fine-grained enough to measure individual neurons. However, we develop an alternative way to determine whether the same neurons support vision and memory without having to measure individual neurons at all.

1.4 Using EEG to Test the Strong Sensory Recruitment Hypothesis

Electroencephalogram (EEG) records the electrical signals discharged from neurons firing through the scalp (see Figure 1.4). The signal from one single neuron is minuscule, but the aggregate signal of many neurons allows for an electrode at the surface of the scalp to detect electrical activity that corresponds to brain activity (Millet, 2002). Due to its non-invasive nature, EEG is a far less spatially accurate measurement than fMRI. However, because EEG measures electrical signals, it has a high temporal resolution, providing accurate measures of when brain activity occurred (something fMRI cannot do).

The high temporal resolution of EEG provides a way for researchers to measure the neural signals that correspond to a specific source of visual stimulation. To do so, a visual stimulus is flashed on and off at a certain temporal frequency, such at 10 times per second (10 Hz). This flashing visual stimulus has been shown to cause the neurons responding to that stimulus to respond with a frequency that matches that of the flashing stimulus (Adrian & Matthews, 1934). This phenomenon is known as the *steady state visually evoked potential* (SSVEP; see Norcia, Appelbaum, Ales, Cottereau, & Rossion, 2015 for a review). The neurons firing at this frequency cause a frequency-specific response in the EEG. By mea-

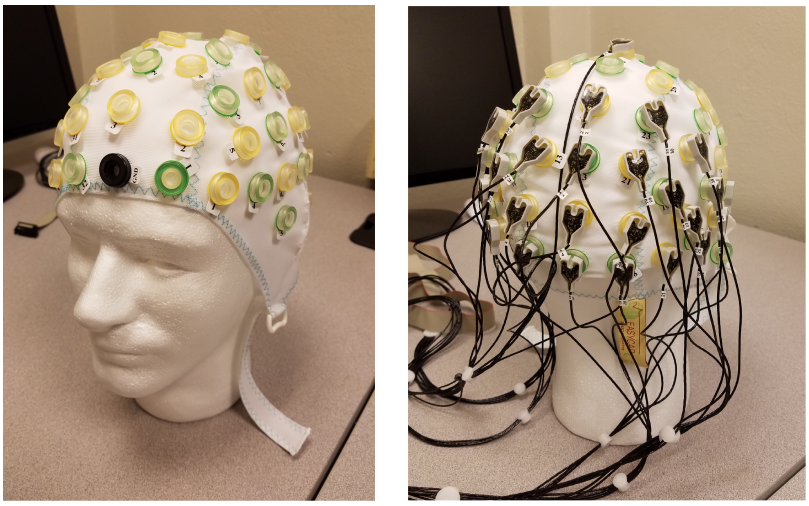

Figure 1.4: EEG cap and electrode configuration

suring the power at this particular SSVEP frequency, the EEG signal provides a measure of how much the brain is responding to the visual stimuli.

The SSVEP approach has been used to study both bottom-up and top-down visual processing. For example, if two stimuli, A and B, are shown simultaneously in two locations that are flickering at different frequencies (e.g. 12 and 18 Hz, respectively), neurons responding to stimulus A will respond at 12 Hz, and those processing stimulus B will respond at 18 Hz. Further, when participants attend to stimulus A, the neural response at 12 Hz increases, and that at 18 Hz decreases. The opposite happens when participants attend to stimulus B (Morgan, Hansen, & Hillyard, 1996). Such demonstrations reveal how top-down processes like attention can alter early visual processing, and how EEG provides a way to measure such effects.

More recently, Garcia, Srinivasan, & Serences (2013) combined the SSVEP paradigm with the "mind-reading" approaches recently used in fMRI, allowing them to decode in-

formation about a viewed stimulus from the SSVEP signal. In particular, the orientation stimulus (such as Figure 1.2) was tagged with a frequency by reversing the contrast 21.25 times per second. A model was then trained to decode which of the nine line orientations the participant was viewing. This parallels Harrison and Tong's previous fMRI study, but now allows for the ability to track the contents of the visual system in real time.

The goal of our study is to use the SSVEP and decoding approach to test the sensory recruitment hypothesis. To do so, we first showed participants an oriented grating stimulus (see Figure 1.2) and asked them to remember its orientation during a subsequent retention interval. During the retention interval, a visual noise stimulus (See Figure 1.5) was flashed on and off at a flickering frequency of 10 Hz, driving neurons that respond to the external stimulus at this frequency. We then employed the Garcia et al. (2013) decoding analysis to this SSVEP signal, but instead of attempting to decode details about the visual noise stimulus, our goal was to decode the orientation held in working memory. The noise stimulus did not contain orientation information. Therefore, any successful decoding of the remembered orientation would come from top-down processes. Additionally, the 10 Hz stimulus-driven signal measured must result from neurons that responded to the bottom-up stimulation. Therefore, if we are able to decode the remembered orientation from the stimulus-driven SSVEP signal, the brain must have the same neurons representing both the incoming visual information (isolated to 10 Hz), and the top-down memory signal (which contains orientation information).

The objective of the EEG experiment is to test whether the contents of working memory can be extracted from the signal generated by the visual stimulation. Before this could be

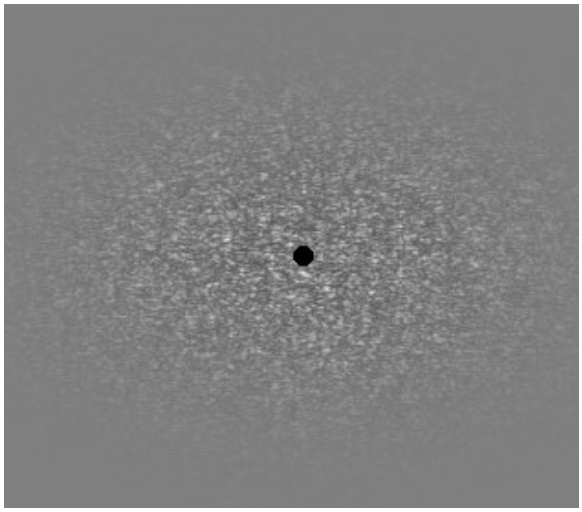

Figure 1.5: Visual noise

tested, we wanted to be sure that the addition of flickering visual noise did not unduly hurt working memory performance.

CHAPTER 2

BEHAVIORAL EXPERIMENT

2.1 Methods

2.1.1 Participants

Fifty undergraduate students at Mississippi State University participated in the behavioral experiment in exchange for credit toward a course requirement. One participant did not complete all trials and was excluded from further analysis.

2.1.2 Procedures

Participants were given the task to remember the orientation of the indicated sine wave grating (see Figure 1.2). Monitors were calibrated (gamma corrected) in all experiments so that the contrast of gratings could be defined. First, participants were instructed to keep their eyes on a central point and to press the mouse button to begin. The central point was a black dot with a radius of 0.2 degrees of visual angle set inside a white circle with a radius of 0.4 degrees of visual angle at the center of the screen. Each trial was randomized from four different conditions in a two by two factorial design: number of sine wave gratings (1 or 6) and visual noise (present or not). The gratings had a radius of 0.75 degrees of visual angle, random phase, and were uniformly oriented 4 degrees of visual angle from the center point starting at 0° (0, 60, 120, 180, 240, 300). The single grating condition was

located randomly at any of the six positions used in the other condition. Stimuli remained on the screen for 50 ms. Depending on the condition, either the prompt or visual noise followed. The visual noise was generated by first making random luminance values for each pixel from a Gaussian distribution and then low-pass filtering this noise (sigma=2.5). The result is visual noise that strongly drives early visual areas with energy that is equal at all orientations (see Figure 1.5). The noise patch had a radius of 2.5 degrees of visual angle and flickered at a frequency of 10 Hz. The visual noise remained on the screen for 1 second. If there was no visual noise, then the screen was blank for the same duration. Following the visual noise or blank screen, a line appeared on the screen for 500 ms indicating a random sine wave grating to remember. The line began at the center of the screen and extended to the center of the grating with a length of 1 degree of visual angle. A response grating would then appear at the center of the screen with the same dimensions as the stimuli. The participants would use the mouse to rotate the grating to the remembered orientation and click to enter the response orientation. Accuracy ranged from perfect (0°) to ±90°. Immediate feedback was given via a bar shown above the central point. The higher and more green the bar, the better the accuracy. The lower and more red the bar, the worse the accuracy.

All reaction times and response errors were recorded. Participants had 20 practice trials and four sets of 120 trials, typically lasting the duration of one hour.

2.2 Results

Figure 2.1 show response errors in differences between studied orientation and response. A sharp peak at 0° response error would indicate near perfect accuracy every time. The height of the peak reflects accuracy, meaning as accuracy decreases, the height of the peak would also decrease. A decrease in accuracy would also indicate an increase in inaccurate responses shown by an increase in the height of the surrounding extreme response errors. Formal statistical modeling analyses are beyond the scope of this paper, but the lack of the notable impact the visual noise had on the results can be seen, nonetheless, in the histogram plots of the participants response error (see Figure 2.1). With no difference between conditions of visual noise, its presence then does not affect VWM and will not be a confounding variable in the EEG experiment.

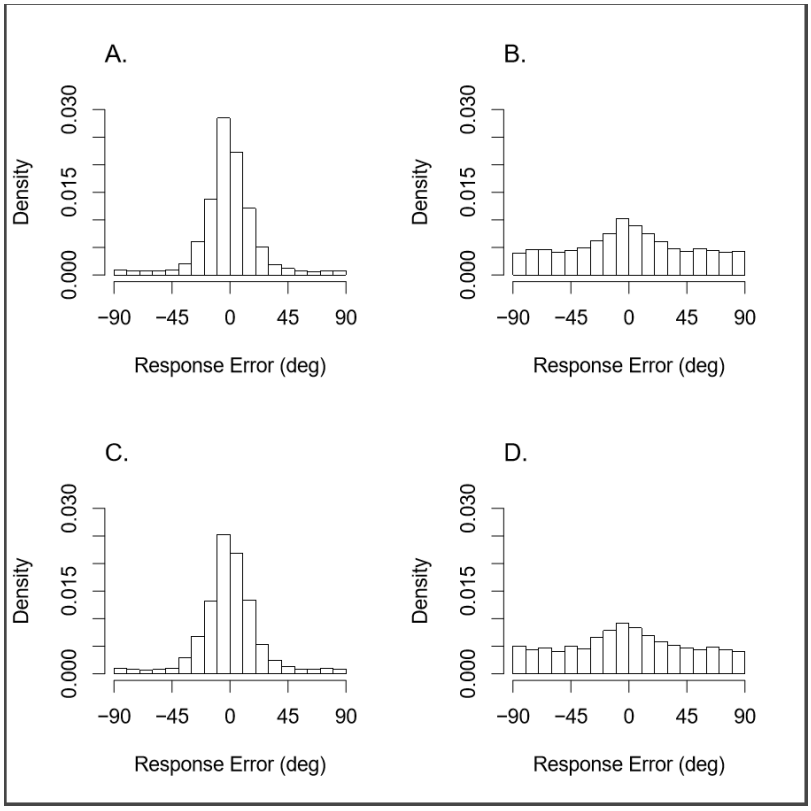

Figure 2.1: Response errors for multiple conditions. A and C both show response errors when participants were shown one orientation on the screen. The histograms for both of these conditions (visual noise vs. no visual noise, respectively) show a high concentration at the middle, indicating participants were responding with a higher concentration of answers closer to 0° response error, i.e. higher accuracy. B and D show response errors when participants were shown six orientations on the screen. The histograms for both of these conditions (visual noise vs. no visual noise, respectively) show a low concentration at the middle with extremities increased accordingly, i.e. greater inaccuracy. This follows the typical capacity of VWM - accuracy decreases when a set size of around four is exceeded (Luck & Vogel, 1998).

CHAPTER 3

EEG EXPERIMENT

3.1 Methods

3.1.1 Participants

Three male and three female students from Mississippi State University ranging from ages 20-28 participated in exchange for monetary compensation ($15 an hour). All participants provided informed written consent in accordance with the Institutional Review Board at Mississippi State University.

3.1.2 Procedures

Participants first had their head measured to use the cap that best fit them. The experimenter would then insert the electrodes in the back of the cap (see Figure 1.4) while explaining what the participant would experience during the capping, what would be required of them during the experiment, and answering any questions they had. After the cap was prepared, the experimenter would place it on the participants head and adjust it to the correct position. Using a flexible tape measure, the cap was positioned so that the center electrode (Cz) was half-way between the ears and half-way between the nasion and inion following the standard positioning for a 10-10 cap. Gel was inserted under the cap at each electrode using a blunt tip needle. The needle would be swirled around to gently graze

the scalp to decrease impedance. Eye electrodes were used to monitor how eye-movement might influence the EEG data. These recordings will be used to ensure that our decoded signals are not being made possible by systematic eye movements, and if not, to remove the noise-inducing eye movements from the other electrodes. The skin around the right eye was cleaned with an alcohol wipe before placing the eye electrodes below and to the side of the eye. During the gelling, the participant was able to do a practice round of the memory experiment to become familiar and understand their task. After this the experiments began.

At the end of the experiment, participants were given shampoo and a towel if they so desired to wash the gel out of their hair, and equipment was cleaned.

3.1.2.1 Vision Task

Participants were instructed to look at the fixation point (a black dot with a radius of 0.25 degrees of visual angle) while sine wave gratings at either 45° or 135° appeared at the center of the screen (see Figure 1.2). Both orientations appeared 15 times each in random order for a duration of 5 seconds and a break of 1.5 seconds between each stimulus. The stimuli had a diameter of 15 degrees of visual angle, a 50% contrast, and a frequency of one cycle per degree visual angle. The phase was assigned randomly and would change 180° every 100 ms tagging the stimulus with a temporal frequency of 10 Hz. Participants' only task was to observe the orientations on the screen. Each block consisted of a total of 30 trials lasting the duration of 3 minutes.

3.1.2.2 Memory Task

Modeled after the Harrison and Tong (2009) experiment, participants were first shown two different sine wave gratings, individually, each for 500 ms. Orientations had a diameter of 15 degrees of visual angle, a 50% contrast, and a frequency of one cycle per degree visual angle. These orientations were displayed in random order and randomly jittered by 3° resulting in line orientations ranging from 42°-48° and 132°-138°. A cue followed for 1 second indicating which orientation to remember. This cue was either "1" or "2" signifying that the first or the second orientation previously shown should be remembered. Both orientations were shown at the beginning to eliminate the possibility of the visual information bleeding into the data pulled while the participant was remembering the orientation. The jitter was added to reduce the consistency of orientations, thereby increasing the need to visualize the orientation rather than remember either "right or left." Visual noise flickered at a frequency of 10 Hz during the time the participant was to visualize the indicated orientation. The visual noise was generated in the same way as the behavioral task, but the diameter was 15 degrees of visual angle and a duration of 8 seconds. Finally, a new grating would show on the screen that was rotated 6° clockwise or counterclockwise from the to-be-remembered orientation. Participants were tasked to indicate whether the new orientation rotated clockwise or counterclockwise relative to the studied orientation by pressing "?" or "z", respectively. Accuracy feedback was shown at the center fixation (same as vision task) by changing to green if correct and red if incorrect. There was a 1.5 second delay until the next trial. There were 16 trials total, 8 of each orientation. Each block also lasted about 3 minutes, but varied in time due to participants response times.

Due to memory tasks requiring more time to complete, fewer trials were completed within one memory task than one vision task. Therefore, participants would complete a vision task followed by two memory tasks to collect about the same amount of data for the vision and memory tasks. The participants typically completed a total 12 tasks (4 vision and 8 memory) over the duration of the 2 hour experiment.

3.1.3 Analysis

EEG data was extracted via Octave and analyzed using R. For the vision tasks, the data were extracted for each trial, including the first 4.5 seconds during which the flashing stimulus was on the screen (see Figure 3.1). This resulted in a 4.5 second sample for each trial and each electrode. For the memory tasks, the data were also extracted for each trial, including the first 7.5 seconds during which the visual noise was on the screen (see Figure 3.2). Similarly, this resulted in a 7.5 second sample for each trial and each electrode. The last half second was not included in data extraction, so as to avoid any possibility of contamination from the following stimulus. In addition to this precaution, eye movements were regressed out of the data so that no outside information could contribute to the decoding of the model.

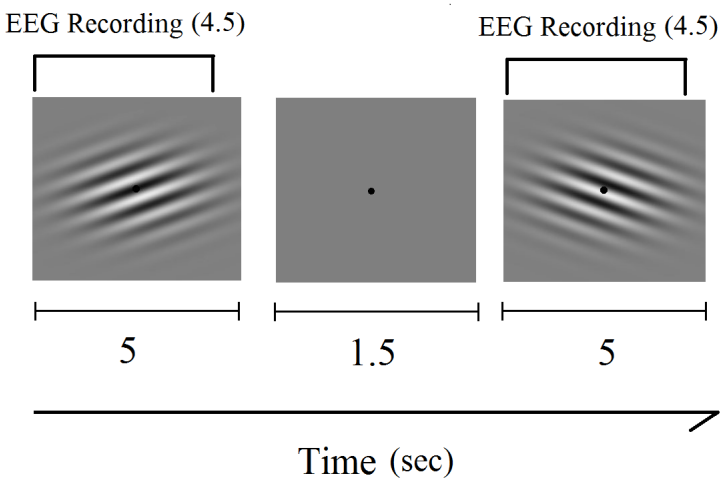

Figure 3.1: Time course of vision task. Sine wave gratings with a temporal frequency of 10 Hz were each shown for 5 seconds followed by a fixation point for 1.5 seconds. EEG data was extracted from the first 4.5 seconds of every grating.

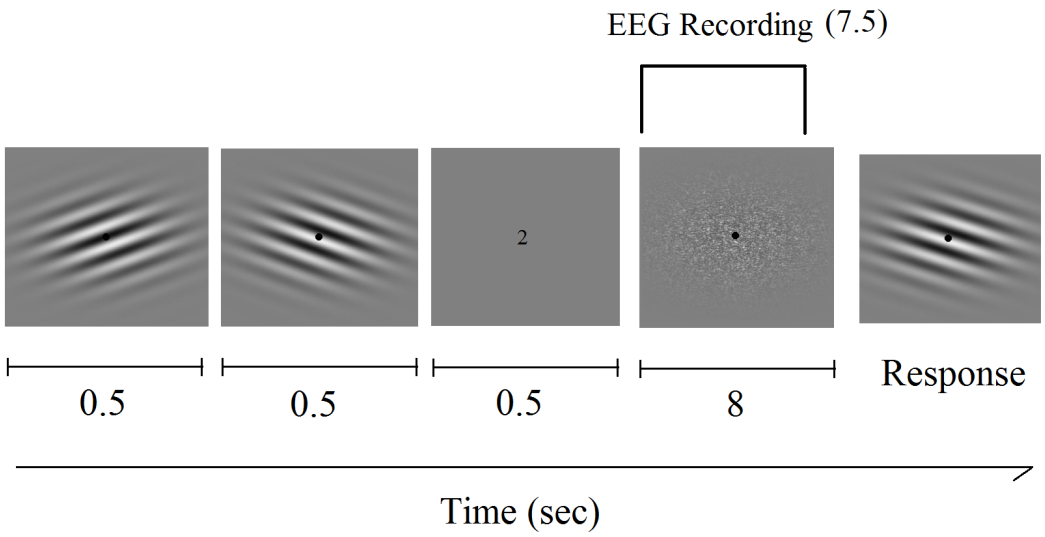

Figure 3.2: Time course of memory task. Both sine wave grating and a cue were each shown for 0.5 seconds followed the visual noise. Visual noise had a temporal frequency of 10 Hz was shown for 8 seconds before the new sine wave grating was shown. EEG data was extracted from the first 7.5 seconds during the visual noise.

The data for each electrode during each trial was first Fourier transformed to convert the voltage time series in the time domain to the frequency domain (see Figure 3.3). Figure 3.4 shows the frequency spectrum for an example participant (averaged over trials and electrodes for one vision block). The spike at 10 Hz is driven by the flickering visual stimulus (SSVEP signal). Power at the harmonics (20, 30, and 40 Hz) of the stimulus frequency are also clearly seen in Figure 3.4. These harmonics are typical of the SSVEP signal (Norcia et al., 2015) and hold meaningful information about the SSVEP just as the

fundamental does (Garcia et al., 2013). From the Fourier transformation, both the power and the phase from the fundamental frequency and the first harmonic were extracted for further analysis.

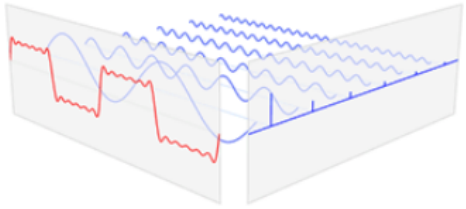

Figure 3.3: Transforming a sinusoidal wave into frequency domain. The sinusoidal wave is broken down into its sine wave components which are then represented by their frequency on the x-axis and power on the y-axis.

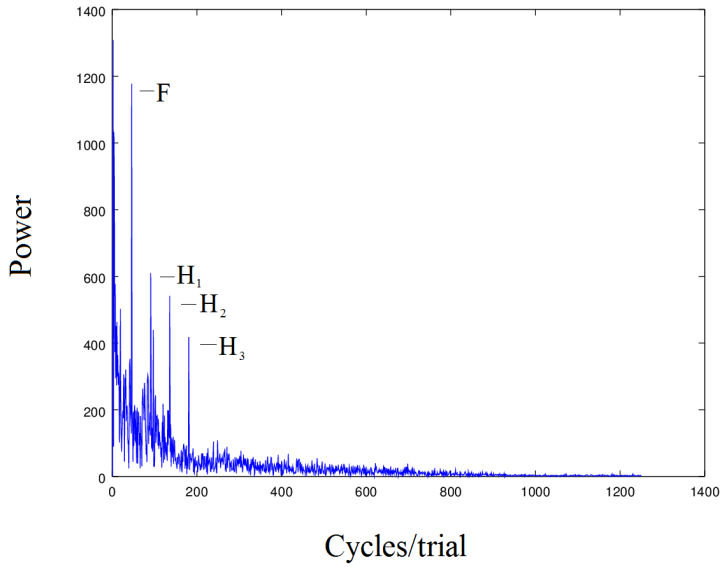

Figure 3.4: Example Fourier transform. This graph shows the Fourier transform from a vision task with the fundamental frequency (F) and harmonics (H) labeled accordingly. The x-axis represents the frequency in cycles per trial. Therefore, the frequency of 10 Hz will be 45 cycles per trial, while the harmonics will be at multiples of 45.

The EEG data was decoded using machine learning, specifically Support Vector Machines (SVM; Cortes & Vapnik, 1995). The SVM formulates a model that can best predict the orientation viewed or remembered for each trial based on the signals from each electrode for that corresponding trial. Figure 3.5 shows a plot of an example model created by SVM. The example data is plotted on a two dimensional field with each axis representing one electrode and the data points representing the voltages of each electrode at that time. The goal of SVM is to fit a model that best separates the two classes of data which is shown in Figure 3.5 as a line dividing the data into two sections: those classified as

"Category A" and those classified as "Category B." The plot represents the points of data that were correctly classified as "O" and incorrectly classified as "X." The models created for this experiment, however, use 29 electrodes, so rather than a 2D plane with a one dimensional line as the model, the actual model has 28 dimensions in a 29 dimensional field. All trials, except for two, one of each stimulus, for all tasks were used to train the model which was then tested on the two remaining trials. The training and testing was reiterated several times so that every trial was used as test data. This was modeled after the analysis of Garcia et al. (2013).

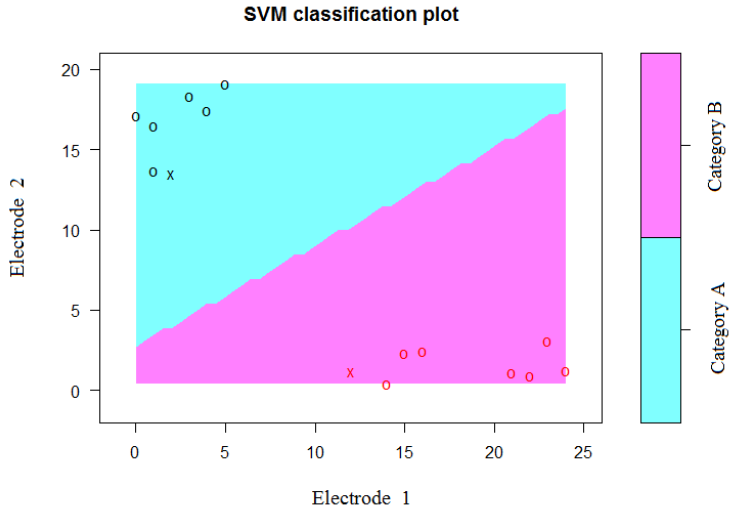

Figure 3.5: Example SVM model. Example data with two support vectors (Electrode 1 and Electrode 2) were given to SVM to create a one dimensional linear model. The model created by SVM is shown by the colors on the plot. Any data in the blue area was classified as "Category A", and any data in the pink area was classified as "Category B." The location of the data represent the voltage of each electrode at that time and are plotted with a symbol representing its accuracy (O = correct, X =incorrect).

3.2 Results

3.2.1 Memory Task Accuracies

Participants on average achieved 82% accuracy (M = .82, SD = .18). This task was designed to be challenging to force the participant to not be able to distinguish whether the new orientation rotated clockwise or counter-clockwise unless they had envisioned the original in their mind as instructed. Because the task was challenging, it was not used as a direct verification of whether the participant was thinking of the correct orientation during the retention interval, and therefore all trials were analyzed, correct or not.

3.2.2 Power Plots

As previously shown in Figure 3.4, the EEG data has an increased power at the SSVEP frequency. This power can be plotted spatially over the scalp at each electrode (see Figure 3.6). The plots show the power of the signal to be strongest towards the back areas for both vision and memory tasks, indicating that these areas were responding to the SSVEP signal for both tasks. This observation aligns with predictions as the SSVEP signal is driven by visual stimulation processed in the occipital lobe at the back of the brain.

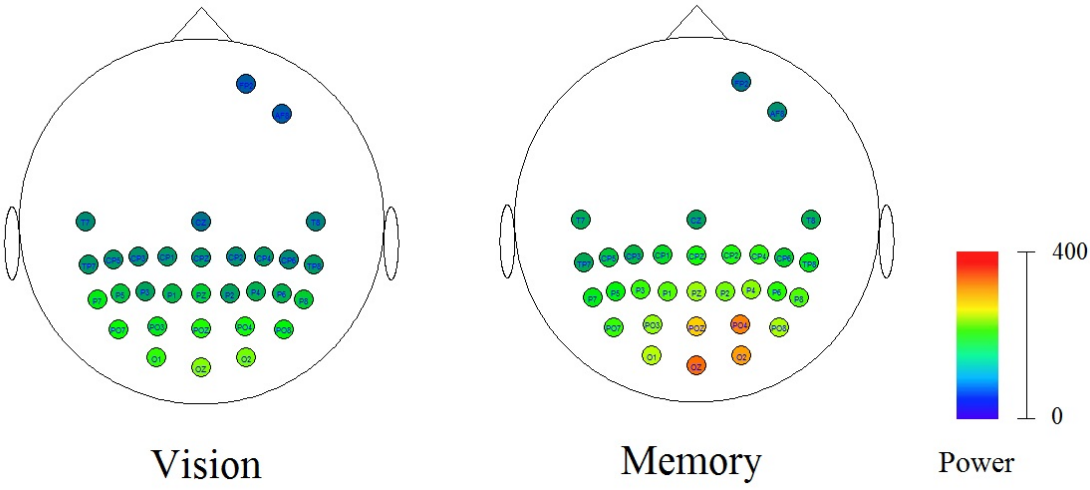

Figure 3.6: Power signal averaged over all subjects. The plots show the location and power of the SSVEP signal of each electrode averaged across all trials and all subjects. The two electrodes towards the front represent the eye electrodes, which also notably have low SSVEP power. The strongest SSVEP power is found towards the back closer to early visual areas.

3.2.3 SVM Model Accuracies

The SSVEP power at each of the 29 locations was used to decode the orientations (see Table 3.1). If no information about the stimulus existed within the data, the model would decode no better than chance (50%). In other words, if the model is just guessing, it could still get about 50% correct. A one sample t-test showed that the model produced accuracies both for the vision task ($t(5) = 4.05$, $p=.01$) and the memory task ($t(5) = 3.17$, $p=.02$) that were significantly greater than chance. This result implies that information about the remembered orientation was present in the SSVEP signal. Although the results show that

the average was above chance, not all subjects' individual accuracies were notably greater than chance as seen in Table 3.1.

Table 3.1: Accuracies

Subject	Vision	Memory
1	70.0%	60.2%
2	55.8%	46.5%
3	65.3%	55.6%
4	56.7%	64.3%
5	66.0%	64.4%
6	53.3%	63.3%

CHAPTER 4

DISCUSSION

Evidence has been provided for the sensory recruitment hypothesis in that the same regions have been shown to carry information for both vision and visual memory. Now, we are asking whether evidence can be found for the "strong" sensory recruitment hypothesis in that the neurons carrying information for both vision and visual memory are the same. Using SSVEP to isolate the activity of neurons responding to external stimulation and SVM to decode information carried with these neurons, orientations held in memory can be predicted. Thus the same neurons responding to external stimuli can be used to decode VWM providing support for the "strong" sensory recruitment hypothesis.

These results still have not unmasked the neural mechanisms underlying the VWM system. The exact same neuron was not isolated and found to be recruited for the same job in both vision and visual memory. Instead, the results indicate the simplicity of one neuron being capable of responding to both outside visual information and inside visual memory. This finding provides profound implications for the VWM system. Two neurons are not necessary to represent both vision and memory. Somewhere in the process there is "cross talk" allowing neurons responsible for vision to also hold information about the contents of VWM. Perhaps visual memory information is passed to visual neurons or perhaps visual

information is passed to visual memory neurons, but at some point our results suggest a meeting of these two types of information.

Beyond unveiling the neural mechanism employed, the paradigm we develop can be utilized for its significant success in predicting information in VWM. With the ability to decode the contents of the mind, possibilities of direct communication with computers becomes more and more of a reality. Applications of such brain computer interface (BCI) have already begun to be put into action. For example, paralyzed patients unable to move are now able to operate prosthetics with nothing but their thoughts, such as controlling robotic arms with EEG (Meng, Beckyo, Olsoe, Baxter, & He, 2016). This mind reading may be nowhere near the abilities of the classic comic book rendition, but it is quickly coming into a power of its own.

In addition to BCI, this paradigm also opens up possibilities for measuring the time course of VWM. Researchers can use this paradigm to answer further questions that were previously unable to be answered without a meaningful time dimension, such as tracing the progression of a memory. Possibly these visual representations are the beginning of memories as we know it, eventually becoming the abstract information filed away into the recesses of our minds, condensed and translated from the initial visual sensation. What was once a visual representation of a sine wave grating became "stripes pointing slightly to the left." Having this capability of measuring the time-course of VWM allows for better understanding of memory systems, the brain areas involved, and the neural connections between them.

This experiment was a first attempt to combine decoding SSVEP and memory. There are many ways that we believe the decoding performance can be improved in future studies. For example, problems with the experiment could have possibly come from participants not thinking of the correct orientation during the visual noise. No indication was built into the experiment for the participant to inform the experimenter that they were not thinking of the correct orientation or maybe not thinking of one at all. The experiment was designed in this manner so as to avoid giving participants an escape to doing the task, but possibly sacrificing the flexibility of accurately labeling orientations for the training of the model. Confidence ratings could be added in future experiments as an indication of whether the participant was thinking of the correct orientation.

Understanding how memory works is a fundamental problem for psychology. Specifically for visual perception, we need to remember what is in front of us every time we move our eyes, which happens several times per second. If we can understand how the visual information is retained during these brief periods, we will have a better understanding of how we see at all.

CHAPTER 5

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