

EEG-MONITORED ELECTRICAL ACTIVITY TO TRACK STORED INFORMATION WITH HIGH TEMPORAL PRECISION

by

RICHARD MCKAY BREUNER

A THESIS

Presented to the Department of Biology
and the Robert D. Clark Honors College
in partial fulfillment of the requirements for the degree of
Bachelor of Science

June 2014

An Abstract of the Thesis of

Richard Mckay Breuner for the degree of Bachelor of Science
in the Department of Biology to be taken June 2014

Title: EEG-MONITORED ELECTRICAL ACTIVITY TO TRACK STORED
INFORMATION WITH HIGH TEMPORAL PRECISION

Approved:  _____

Edward Awh

Because working memory is correlated with measures of fluid intelligence and is relevant on a daily basis, it is important to investigate its properties. By monitoring neural activity with electroencephalography (EEG), we are able to generate channel tuning functions from the electrical waves oscillating in the alpha band frequency (7.5-12.5 Hz). This study seeks to validate the temporal precision allowed with EEG by exploring the sensory systems responsible for governing visual working memory, specifically the manner in which populations of sensory neurons work together to create cognitive representations of relevant features of the outside world. Focusing on the neural activity responding to oriented lines, we found that while visual stimuli invoked equivalent responses for both the relevant and irrelevant orientations when two lines occupied the visual field, an amplitude increase in the tuning functions associated with the relevant feature coincided with an amplitude decrease in tuning functions associated with the irrelevant feature when the subject was asked to hold the orientation in memory. These findings validate the influential role of selective attention on populations of orientation-selective neurons.

Acknowledgements

I would like to thank Professor Awh, Professor Black, and David Anderson for helping me to fully examine the specific topic and consider the various perspectives and contexts related to this subject matter. I would like to express my sincerest gratitude for having the privilege of having excellent professors willing to guide me through this strenuous but rewarding process. I would like to thank David Sutterer and Joshua Foster for answering my numerous questions throughout my time working in the Awh Lab. I would like to thank the Vogel Lab and the Mayr Lab for providing a friendly atmosphere to both work and relax in. I would finally like to thank my brother Jupiter, my sister Maggie, my dad Joe, my mom Cora, and my dog Fez for providing a rock-solid foundation to build upon.

Table of Contents

Introduction	1
Methods	10
Results	15
Discussion	19
Bibliography	22

Introduction

In order to actively hold multiple pieces of ephemeral information in the mind, one activates their working memory. Working memory is a part of short-term memory that focuses on the active storage and online manipulation of information over a short period of time. Baddeley and Hitch (1974) proposed a model claiming that working memory is made up of buffers, each with specific responsibilities for coding information. There is a buffer storing verbal information, a buffer storing visual or spatial information, and a buffer responsible for storing episodes, all of which extract information occurring in the outside world in real time or from long-term memory. An everyday example of accessing working memory is a phone number. The ears hear a phone number and send signals to the brain, which analyzes this information, then stores it so as to easily access the information soon afterwards.

Just as humans are unique in physically observable traits like gender, ethnicity, or height, capacity limits and precision of working memory varies among individuals. Studies have shown that visual working memory has a capacity limit of about three to four items (Luck and Vogel, 1997), and a fixed amount (~3-4) of objects are maintained in working memory regardless of item complexity (Awh, Barton, and Vogel, 2007). Working memory capacity is relevant due to its correlation with measures of fluid intelligence, such that generally the more items one can hold in memory, the greater their fluid intelligence (Fukuda, Vogel, Mayr, and Awh, 2010). As humans reach their working memory capacity, the precision, or resolution of items held in working memory, declines (Anderson, Vogel, and Awh, 2011). In addition, there are reliable

individual differences in the quality or precision of the representations in visual working memory.

Low-capacity individuals have a more difficult time preventing irrelevant items occupying their visual field from engaging sensory representation, while high-capacity individuals frequently and efficiently ignore irrelevant information such that relevant stimuli dominate their working memory (Vogel, McCollough, and Machizawa, 2005). Subjects with high working memory capacity are not as susceptible to attentional capture hindrance, which indicates the ‘capture’ of attention by an irrelevant feature. Recent work has sought to ascertain the elemental difference in attentional control, specifically a study undertaken by Fukuda and Vogel (2010) in which both high- and low-capacity individuals showed equivalent attentional capture hindrance in the period directly following attentional capture. However, they found that high-capacity subjects were quicker to recover and revert back to the relevant item than low-capacity subjects, suggesting that the efficient attentional control associated with high-capacity subjects is due to quick disengagement from distractors. Both relevant and irrelevant objects in a trial elicit neural responses so long as both items occupy the visual field.

One of the emerging concepts regarding working memory—suggested by both unit recordings from nonhuman primates (Pasternak and Greenlee, 2005; Super, Spekreijse, and Lamme, 2001) and also human neuroimaging studies (Riggall and Postle, 2012; Ester, Serences, and Awh, 2009; Harrison and Tong, 2009; Serences, Ester, Vogel, and Awh, 2009) is that the maintenance of items in working memory is governed by sensory recruitment. This theory postulates that the same mechanisms maintaining working memory encode the information we wish to store and access. This

information is characterized by unique features that elicit unique responses from different sensory systems. Feature-selectivity is an inherent quality of sensory systems that not only provides a manner by which to group millions of neurons but also changes based on the cortical area in which the neurons are located. Different areas of the brain require different stimulus attributes to be activated, and this study focuses on neurons associated with the visual system such that visual stimuli elicit recruitment of particular populations of sensory neurons. For example, neurons associated with the retina, or the layer at the back of the eyeball, prefer small spots of light, neurons associated with initial stages of visual cortex (primary visual cortex, or V1) prefer oriented lines, and neurons associated with later stages prefer complex items like faces. This suggests that these neurons in the face-selective regions of inferotemporal (IT) cortex display prolonged increases in activity when an observer holds a face in working memory (Chelazzi, Miller, Duncan, and Desimone, 1993; Miller, Li, and Desimone, 1993; Ranganath, Cohen, Dam, and D'Esposito, 2004). While V1 neurons respond the strongest to one specific orientation, they emit an admittedly weaker signal when presented with a line slightly differing from the preferred orientation. Thus, orientation-selectivity is a type of feature-selectivity in the recruitment of populations of V1 neurons.

A population code is the superlative way to depict the sensory recruitment of populations of feature-selective neurons. In an ideal world, the activity of one neuron in response to a unique stimulus would never change such that inferring the preferred stimulus attributes of that neuron would be relatively simple. However, sensory neurons are noisy (characterized by activity that is not relevant to the stimulus) and the

firing rate triggered by identical stimuli varies across repeated trials. This is why responses from millions of neurons are pooled together to generate a population response profile that can be employed to ascertain the approximate details of the stimulus in question despite the presence of physiological noise. The neurons in primary visual cortex (V1) are often classified into one of two types of cells based upon their preferences surrounding oriented lines (Hubel and Wiesel, 1962). While both simple and complex cells have specific orientation preferences, simple cells prefer oriented lines in a specific location in the visual field. Both types of cells make up the sensory systems recruited to generate an accurate population code.

One of the most common methods for observing neural activity in humans is functional Magnetic Resonance Imaging (fMRI). Functional MRI findings lend credit to the sensory recruitment hypothesis in that activity in sensory regions encodes the stored orientation during a working memory delay period. Functional MRI measures brain activity by detecting associated changes in blood flow, driven by the fact that cerebral blood flow is a consequence of neuronal metabolic activity. A voxel is a unit of measurement in the brain that individually represents the activity of a population of neurons in three-dimensional space. Serences, Ester, Vogel, and Awh (2009) found patterns of activity in visual cortex that predicted the online contents of working memory. They presented the subject with an oriented grating for one second, asked the subject to hold that orientation in memory for ten seconds, then presented another oriented grating and asked the subject to indicate if the second grating matched the first grating. Using fMRI, sustained activation patterns representing the intentionally stored orientation of a multi-faceted object were localized to primary visual cortex (V1) during

the working memory delay period. Initially, the signal did not contain any information suggesting an increase in activity. Multi-voxel pattern analysis (MVPA) is necessary for distinguishing the neural regions that maintain working memory by concentrating on changes in activation patterns rather than simply alterations in the average amplitude of the blood-oxygenation-level-dependent (BOLD) response. The activity increase became apparent only after employing an MVPA on the data. The distribution of orientation-selective cells in voxels is what lets this analysis work.

As an extension of the Serences et al (2009) study, Ester, Anderson, Serences and Awh (2013) reconstructed orientation-selective population response profiles by manipulating fMRI and MVPA as well. After entering an fMRI machine, participants were presented with an oriented grating for one second, held that orientation in memory for twelve seconds, and were finally given three seconds to adjust a new grating to the orientation of the initial grating. They generated population response profiles whose amplitudes were the most robust for the remembered orientation and gradually fell as the angular distance from this orientation increased. Supporting sensory recruitment, their findings suggested fMRI is a good tool for localizing population codes.

It has been shown that cognitive performance was reduced when visual stimuli appeared in different locations in the visual field (Zaksas, Bisley, and Pasternak, 2001; Hollingworth, 2006, 2007), suggesting feature representations maintained by working memory are spatially local and sensory recruitment is limited to the neural regions retinotopically mapped to the receptive field location occupied by the visual stimulus. However, recent evidence generated from fMRI and MVPA shows that neuronal activation responding to an intentionally remembered feature was present in both

regions of contralateral visual cortex mapped to the position of the remembered object and also to regions of ipsilateral visual cortex that were not mapped to the section of the visual field containing the stimulus (Ester, Serences, and Awh, 2009). This contradicts the hypothesis that working memory maintenance is spatially local, suggesting instead a spatially global sensory recruitment that may strengthen working memory precision through a more robust coding of the visual stimulus.

The other primary method for analyzing neural activity and generating population codes is electroencephalography (EEG). While fMRI is useful for localizing activity to distinct areas of the brain, it lacks the temporal precision that characterizes EEG. Putting this into context, fMRI monitors activity every 2 seconds, while EEG monitors activity every 4 milliseconds. Combined with previously acquired spatial knowledge of the brain using fMRI, the temporal knowledge allowed with EEG gives accurate information as to where and when activity for a given feature occurs. Whereas fMRI observes the BOLD response generated by blood flow, EEG measures electrical activity by recording voltage fluctuations on the skin/scalp that correspond to changes in ionic currents inside the brain. Garcia, Srinivasan, and Serences (2013) described population codes with EEG showing this 4 ms temporal resolution, a vast improvement to the lag between neuronal activation and cerebral blood flow utilized by fMRI. In each 3,000 ms trial, the subject was presented with a centrally located stream of letters surrounded by an oriented grating. They were asked at the end of each trial if the orientation had shifted clockwise or counterclockwise. The response profiles they generated were based on the spatially distributed sequence of steady-state visual evoked potential (SSVEP) responses to flickering visual stimuli. In this Garcia et al

experiment, they concentrated their analysis on the magnitude of the second harmonic of the flickering grating (42.5 Hz).

Although the optimal frequency used in the Garcia et al. (2013) study corresponded with the physical flicker frequency of the stimulus display (42.5 Hz), many EEG studies take advantage of endogenous neural rhythms. EEG is composed of summed activity across multiple frequencies, but I am interested in waves oscillating between 7.5 and 12.5 Hz. This frequency range is titled the alpha band and consists of neural oscillations arising from synchronous and coherent electrical activity. Perhaps due to the correlation between the two, Hans Berger both discovered alpha waves and invented EEG in 1924 (Haas, 2003). It is in the alpha band frequency range that it will become apparent if the subjects participating in my experiment are able to ignore irrelevant features of the visual stimulus such that the target orientation dominates working memory.

Alpha band modulation is linked with both cued ignoring and cued attending of visual stimuli, suggesting the importance of alpha band oscillations to deployment of selective attention (Payne, Guillory, and Sekuler, 2013). Just like the population response profiles necessary to overcome physiological internal noise, perceptual mechanisms are in place to deal with the competition in the sensory input stream that arises when multiple objects occupy the visual field. Because the brain has a limited capacity for processing visual stimuli (Awh, Barton, and Vogel, 2007), sensory inputs compete for representation in cortex (Desimone and Duncan, 1995; Reynolds and Desimon, 1999; Tsotsos, 1997). Though this appears a subconscious cognitive competition, humans have a certain amount of conscious control over the response

activity of populations of neurons. This is deemed top-down control and plays a large role in selective attention. Under the assumption that perception is extracted from neural population codes, empirical studies have indicated that top-down attentional control distinguishes competing visual inputs in order for relevant stimuli to dominate sensory representation such that irrelevant stimuli are actively ignored (Borst and Theunissen, 1999; Paradiso, 1988; Pouget, Deneve, and Latham, 2001; Shadlen, Britten, Newsome, Movshon, 1996). It is in the population response profiles generated from alpha band oscillatory activity that it becomes apparent when the subject successfully overcomes the attentional capture hindrance and allows the target orientation complete access to working memory.

Neural responses to visual stimuli processed and analyzed by electrodes on the scalp and face are often categorized into either evoked or induced responses. Generally, evoked activity refers to activity that is phase-locked to the stimulus onset while induced activity refers to oscillatory activity regardless of its phase. The evoked response processes activity from multiple trials and eliminates noise evident in individual trials. One oscillatory wave cycle has many phase values, and the evoked response has a common phase value with respect to onset of stimulus. My study focuses on induced activity in the alpha band because it is this neural signal that contains information about the stored item during the delay period of the memory task.

Previous work (Serences et al, 2009) has identified that selective attention biases neural population response profiles so as to favor populations of neurons that represent behaviorally relevant items. One aim of my study was to determine if this same neural population response profile bias stemming from selective attention would be present

when a distractor orientation (green) was similar to the angle of the target orientation (blue). Specifically, I looked to verify if the activity observed when both oriented lines were presented on a computer screen in the subject's visual field differed significantly than during a delay period when neither line was on the screen and the subject was asked to maintain the target orientation in memory. It is in this transition from sensory to delay period that I wish to examine the temporal profile of orientation tuning as a result of attentional control. We hypothesized that the stimulus will invoke channel responses for both the target and distractor orientations during the sensory period. Additionally, channel responses for the target orientation will increase in amplitude during the maintenance (delay) period, coinciding with a substantial decrease in amplitude of the channel responses for the distractor orientation. This would indicate that during the period in which the subject is asked to hold the target orientation in memory, the distractor orientation is not stored and subsequently does not induce any significant neural activity. Furthermore, the spontaneous activity visible during the inter-trial interval (ITI), or the period between subject-induced trial initiation and the presentation of the two oriented lines, should provide a baseline with which to compare the increased target activity and decreased distractor activity throughout the maintenance period.

Methods

Participants

29 undergraduates from the University of Oregon participated in the study compensated financially at \$10/hour. All participants were free of extraneous health concerns and possessed normal visual acuity. Additionally, each subject gave informed consent according to procedures governed by the University of Oregon Institutional Review Board.

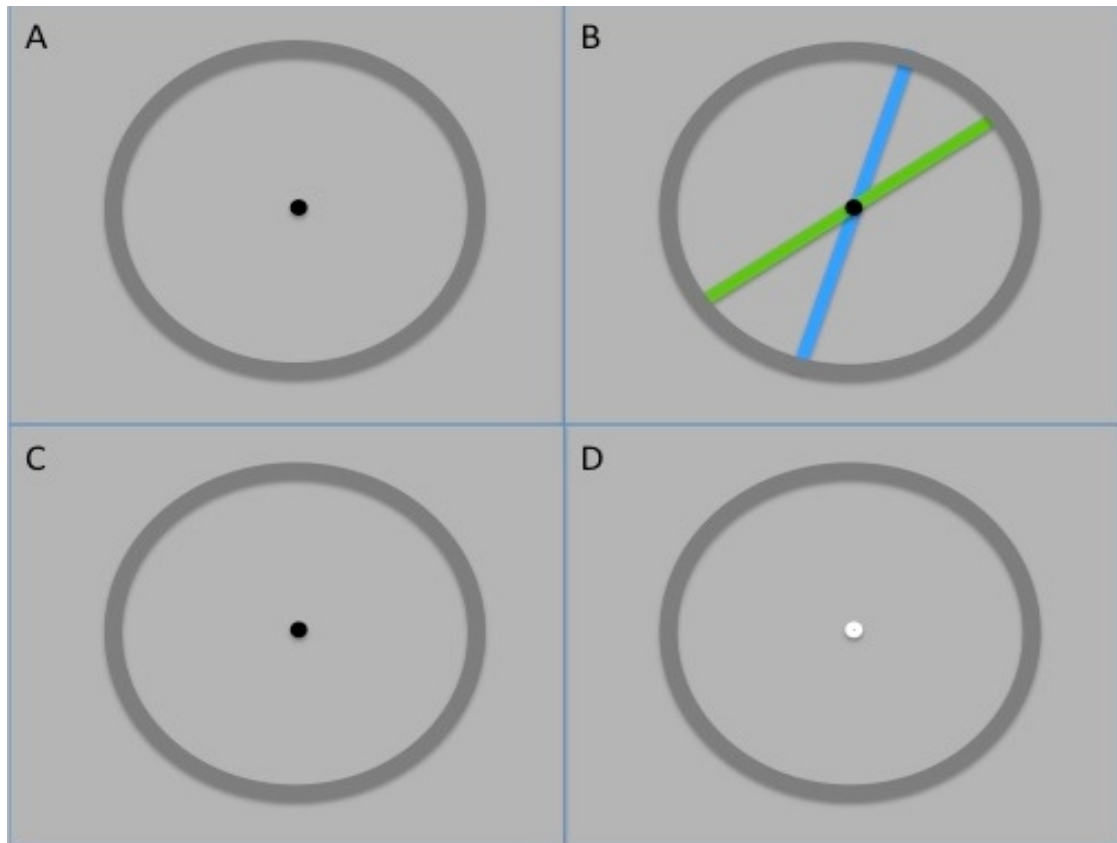


Figure 1: Sample of visual stimulus for 1 trial. A) ITI display screen appearing from depression of space bar to appearance of oriented lines, 0-1400 ms after trial onset. B) Oriented line display screen appearing from 1400 ms-1650 ms after trial onset. C) Delay period screen appearing from 1650 ms-2800 ms after trial onset. D) Recall screen appearing 2800 ms after trial onset, indicated by a white fixation dot

Stimuli Displays

Using the Psychophysics Toolbox extension (Brainard, 1997; Pelli, 1997), stimuli were created in MATLAB (MathWorks) and presented on a 17-inch flat cathode ray tube computer screen (refresh rate of 120 Hz). Viewing distances were ~100 cm. Stimuli were presented on a grayscale display (RGB=[145,145,145]), and participants fixated on a central black dot that subtended 0.3° by 0.3° of visual angle.

Participants observed and remembered the orientation of a solid bar bridging the diameter of a centrally displayed ring (Fig. 1B). The length (ring diameter) and width (ring thickness) were 7.1° and 0.6° of visual angle, respectively. Two bars (one target, one distractor) were depicted in isoluminant blue (RGB=[0,150,200]) and green (RGB=[0,162,0]) and the ring was rendered in dark gray (RGB=[125,125,125]).

For each trial, stimulus orientation was randomly presented from one of eight orientation bins spanning 0 - 157.5° in 22.5° increments, with jitter added ($\pm 11.25^\circ$) to cover all 180° of possible orientation space and prevent categorical coding of the orientations. In addition to the balanced presentation of orientation bins within each block, orientation differences between the target and distractor lines were fully counterbalanced within each block.

At the end of the delay period in each trial, participants were cued by the change of fixation from black to white to recall the target orientation by using a computer mouse to click on a point along the perimeter of the ring associated with said orientation.

Procedure

The experiment took roughly 2 hours to complete, and was composed of 10 blocks of 64 trials each. On a computer screen directly in front of the subject, the subject was instructed to either remember the blue or green orientation. After depressing the space bar to proceed in the experiment, there is an ITI display consisting of just the gray ring and black fixation (Fig. 1A) for 1400 ms. Next, a green line and a blue line each with different orientations (Fig. 1B) flashed up for 250 milliseconds.

Next is a delay period from 1650 milliseconds after trial onset (space bar depression) to 2800 milliseconds after onset (Fig. 1C) in which the subject is required to store and maintain the correct orientation while ignoring the distractor orientation. At 2800 milliseconds, the fixation dot changes from black to white indicating termination of the delay period and onset of the recall period. Subjects indicated target orientation by clicking a point on the ring they deem closest to the target.

Channel Tuning Functions

This study seeks to investigate the recent computational advances that allow researchers to efficiently decode and model the orientation selectivity represented throughout various cortical regions of the visual system. There is a nonuniform distribution of orientation-selective cells read by each sensor, which in the case of EEG are the electrodes, allowing for the characterization of the essential neural response. Using the forward encoding model (Brouwer and Heeger, 2009), we can summate the orientation-selective responses that constitute the average activity processed by each sensor. The alpha waves are processed by the spatially global sensors that process the combined neural activity of a group of cells. If these cells possess orientation selectivity, it will become apparent in the analysis of the readings generated by the sensors.

Each sensor maintains a greater number of cells preferring one orientation, evidenced by the stronger amplitude of activity for that orientation relative to others. For example, if the preferred angle is 0 degrees represented as a vertical line, the group of neurons will fire most strongly at 0 degrees with a diminishing response strength as the presented angle moves further away from 0. fMRI records from hundreds of

sensors, which in the case of fMRI are voxels, simultaneously so as to display that each voxel responds more to a given orientation due to the nonuniform distribution. Garcia et al (2013) utilized fMRI but also extended this method into EEG, demonstrating above-chance classification of stimulus values based on the response profiles of each sensor to a complete set of varying stimuli. The differential activity responding to a unique orientation allows one to insinuate the relative contribution of orientation-selective cells to the perceived neural response. The recent computational advances allow for the creation of a channel tuning function, which accurately depicts the underlying population code.

In order to simplify raw neural data incorporating all 180° , we divide neural population preferences into 8 categories, or channels at 22.5° each. These channels act as bins in the channel tuning function that group angle preferences among neurons. If the x-axis plots angle preference, it is common to assume the 8 channels would generate tuning functions that looked like 8 different bell curves functioning based on individual preferences. To solve this, the forward encoding model is employed, which assumes that a given neural response is a product of the weighted linear sum of 8 idealized tuning functions, each centered over the preferred stimulus channel. This allows for the mapping of neural responses into hypothetical tuning space using a weight matrix. The reason for presenting the data from each channel collectively is to produce a larger peak in the middle and a more pronounced diminishing response strength to the left and right.

Results

While 29 subjects participated in my study, 4 of them produced data enshrouded with artifacts resulting from both unnecessary eye movements and an increased amount of noise, leaving me with 25 sets of data to evaluate. I hypothesized that while the stimulus will invoke channel responses for both the target and distractor orientations during the sensory period, channel responses for the target orientation will increase in amplitude during the maintenance (delay) period, coinciding with a substantial decrease in amplitude of the channel responses for the distractor orientation. The results supported my hypothesis, as there was indeed visible neural induced activity associated with both target and distractor orientations during the sensory period, supporting the previous finding that the oscillatory waves characterizing the induced activity contains the most critical information for this study. It is in the maintenance period that sensory recruitment works to simultaneously maintain working memory and encode the target orientation. Subjects employed top-down selective attention to attend to the target orientation and ignore the distractor orientation, evidenced by the induced activity that was selective to the target during the maintenance period. It is in this maintenance, or delay, period that the mean amplitude for activity correlated with the target orientation increased as the mean amplitude for activity correlated with the distractor orientation essentially vanished.

Figure 2 depicts the evidence necessary to indicate the temporal precision for which EEG was employed in this study. Fig. 2 depicts tuning functions for the target orientation and activity associated with the distractor orientations, but it also depicts how the data change over time. Time “0” indicates the instant both target and distractor

orientations occupy the visual field and does not include the 1400 ms ITI immediately following subject-induced trial initiation. The translucent frame located at 250 ms in both 2A and 2B indicates both the moment the stimulus no longer occupied the visual field and also the onset of the maintenance period. The red peaks centrally located in Fig. 2 indicate the mean amplitude peaks and the steady transformation to blue represents the diminishing graded response profile. During the sensory period (0-250 ms poststimulus) when both lines are presented to the subject, the target and distractor orientations show tuning functions, albeit tuning functions with small amplitudes relative to the pronounced peaks during the maintenance period in Fig. 2A. Fig. 2A depicts the pronounced tuning functions for the preferred orientation evident in the maintenance period (250-1400 ms poststimulus), tuning functions that are absent in the maintenance period of Fig. 2B. Though ultimately insignificant to this study because of its qualitative nature, it is interesting that the pronounced tuning functions representing the target orientation do not reach peak amplitude until ~750 ms poststimulus.

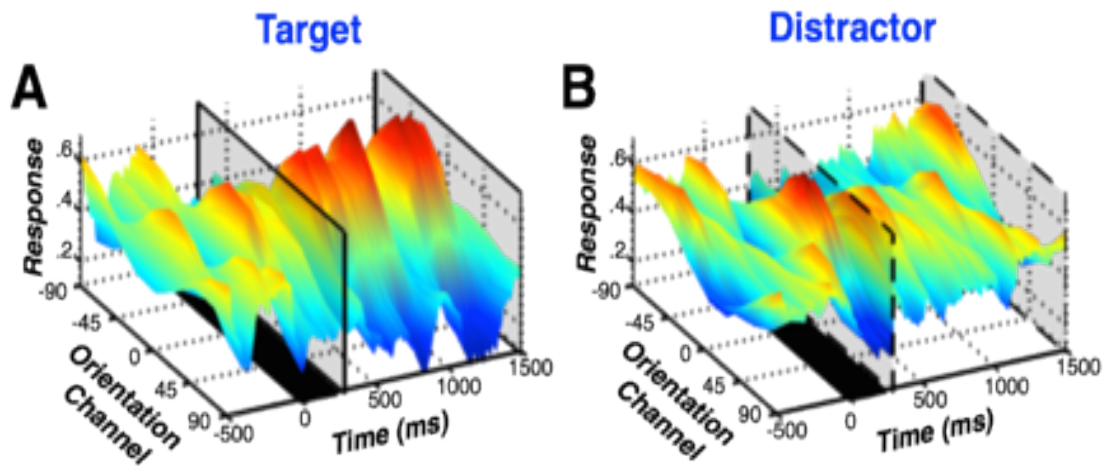


Figure 2: Induced channel response for both target and distractor orientations over time, with the centrally located red peaks indicating an increase in mean amplitude of neural activity and the blue valleys indicating a decrease in mean amplitude of neural activity. A) Visible activity associated with the target orientation evident during the sensory period (0-250 ms poststimulus) and the maintenance period (250-1400 ms poststimulus). B) Observable activity associated with the distractor orientation slightly visible during the sensory period but absent during the maintenance period.

Figure 3 depicts the data averaged across all trials so that it includes the tuning functions associated with each one of the 8 channels. The point on the x-axis indicated by “0” refers to the orientation channel that matched the stored orientation on each trial. With that in mind, this data is concurrent with previous data in that greatest channel activity is observed for the channel that matches the stored orientation, and channel activity decreased with each step to the left and right of this peak. Orientation channels do indeed respond the strongest to a specific preferred orientation, yet they still fire to orientations that stray from the preference, albeit with diminishing amplitude.

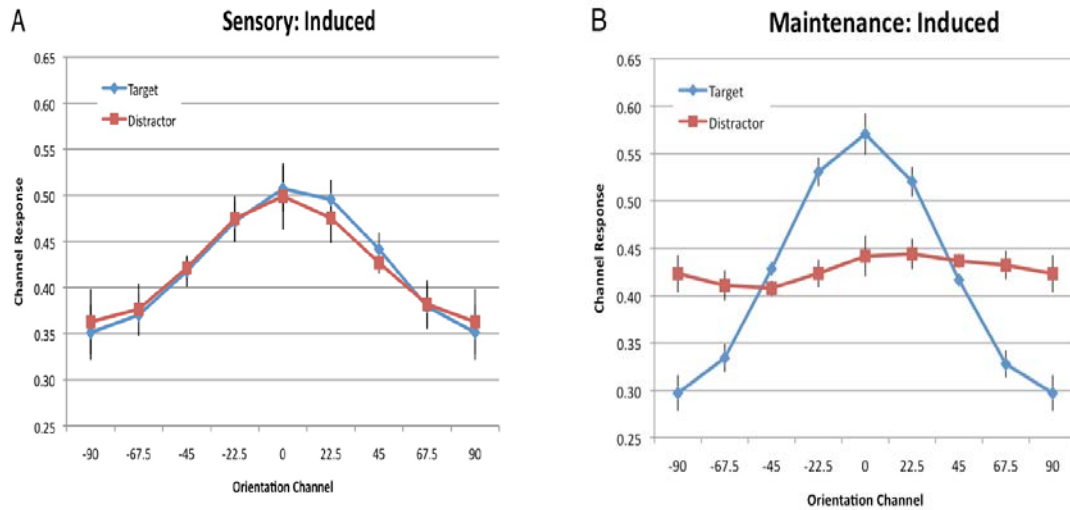


Figure 3: Mean amplitude of the induced response in primary visual cortex (V1) for both the target and distractor orientations. A) Electrical activity for the sensory period when both lines occupy the visual field. B) Electrical activity when neither line is in the visual field and the subject is asked to hold the target orientation in memory.

The sensory activity visible in Fig. 3A suggests a stronger response to the target orientation due to the more pronounced peak relative to the mean amplitude of the distractor orientation response. However, this difference in response strength was not significant, leading to the conclusion that both orientations are processed when relevant and irrelevant stimuli occupy the visual field. Figure 3 does provide significant evidence related to one aim of this study in that the mean amplitude of neural oscillations associated with the target orientation increased during the maintenance period when the subject intentionally maintained that orientation in memory. Because a greater amplitude indicates a more robust representation of the associated feature in memory, this evidence supports the selective attention theory (Serences et al, 2009) and thus indicates that subjects were focused on the target orientation. EEG is an applicable method for monitoring the electrical activity encoding stored information with high temporal precision.

Discussion

These results demonstrate that working memory is responsible for initially processing and maintaining items occupying the visual field while selective attention is responsible for biasing neural populations towards behaviorally relevant features. In line with the sensory recruitment hypothesis, the data-driven channel tuning functions generated in this study reflect the simultaneous activity of millions of orientation-selective neurons. This spatially global recruitment of individual sensors allows for EEG-monitored electrical activity to accurately represent details of the visual stimulus in question. The graded response profiles in the channel tuning functions validate this spatially global recruitment, as populations of neurons still activate in response to oriented stimuli that differ from their preference, albeit with lower robustness. The EEG-monitored electrical activity necessary to my study oscillates in the neurologically natural alpha band frequency (7.5-12.5 Hz) and not in the oscillatory frequency of an experimentally induced flickering stimulus (Garcia, Srinivasan, and Serences, 2013).

Because alpha band modulation encodes both behaviorally relevant and irrelevant items (Payne, Guillory, and Sekuler, 2013), the induced activation patterns in this frequency correlated with WM maintenance during the delay period. Though the alpha band contains both induced and evoked activity, it is the induced activity we are interested in because it is highly informative to the evidence of working memory processing during the delay period. It is the subject-induced top-down control of selective attention that leads to the domination of relevant stimuli in the competition for sensory input representation in cortex. While previous work has provided a foundation of knowledge regarding the graded response profiles, this study has furthered the notion

that EEG is an effective means to generate channel tuning functions characterized by both high temporal precision and also informative evidence regarding memory storage.

The amplitude of the feature-selective response profiles and the temporal precision allowed by EEG gives information as to what the subject is holding in mind at a given time and can also be used to predict behavioral performance on store-and-drop tasks. Ideally, future research would investigate the strength and consistency of selective attention in discriminating similar features in a repetitive context. Presented with an identical visual stimulus (Fig. 1), the subject would be instructed to attend to the green orientation nine trials in a row, but on the tenth trial they would be instructed to ignore the green orientation and instead target the blue orientation. Research has shown that populations of neurons can be conditioned in their responses to varying stimuli (Arduin, Fregnac, Shulz, Ego-Stengel, 2013; Fetz, 1969; Fetz, Finocchio, 1971), leading to a potential hypothesis that the green orientation would be harder to ignore on the tenth trial.

Although we did not evaluate individual data on a subject-by-subject basis in this study, it would be interesting to execute this analysis in an equivalent future experiment so as to further explore hypothetical differences in attentional capture hindrance between high- and low-capacity subjects. Another manipulation could involve the number of oriented lines presented at onset. This would tap into the aforementioned memory capacity in regards to the number of items subjects can attend to at the same time. Presenting the subject with three lines instead of two would be a simple way to exercise this manipulation.

In summary, these findings demonstrate the millisecond-by-millisecond temporal precision allowed by monitoring neural activity with EEG. Additionally, the results suggest that while visual stimuli invokes equivalent channel responses for both the target and distractor orientations during the sensory period, an amplitude increase in electrical activity tuned to the target feature coincides with an amplitude decrease in electrical activity tuned to the distractor feature during the maintenance period, validating the influential role of selective attention on populations of orientation-selective neurons.

Bibliography

- Anderson, D. E., E. K. Vogel, and E. Awh. "Precision in Visual Working Memory Reaches a Stable Plateau When Individual Item Limits Are Exceeded." *Journal of Neuroscience* 31, no. 3 (2011): 1128-1138.
- Arduin, P.-J., Y. Fregnac, D. E. Shulz, and V. Ego-Stengel. "'Master' Neurons Induced by Operant Conditioning in Rat Motor Cortex during a Brain-Machine Interface Task." *Journal of Neuroscience* 33, no. 19 (2013): 8308-8320.
- Awh, E., B. Barton, and E. Vogel. "Visual working memory represents a fixed number of items regardless of complexity." *Journal of Vision* 7, no. 9 (2007): 352-352.
- Baddeley, Alan. "The episodic buffer: a new component of working memory?." *Trends in Cognitive Sciences* 4, no. 11 (2000): 417-423.
- Borst, A, and FE Theunissen. "Information Theory and Neural Coding." *Natural Neuroscience* 2 (1999): 947-957.
- Brainard, David H.. "The Psychophysics Toolbox." *Spatial Vision* 10, no. 4 (1997): 433-436.
- Brouwer, G. J., and D. J. Heeger. "Decoding and Reconstructing Color from Responses in Human Visual Cortex." *Journal of Neuroscience* 29, no. 44 (2009): 13992-14003.
- Chelazzi, Leonardo, Earl K. Miller, John Duncan, and Robert Desimone. "A neural basis for visual search in inferior temporal cortex." *Nature* 363, no. 6427 (1993): 345-347.
- Courtney, Susan M., Leslie G. Ungerleider, Katrina Keil, and James V. Haxby. "Transient and sustained activity in a distributed neural system for human working memory." *Nature* 386, no. 6625 (1997): 608-611.
- Desimone, Robert, and John Duncan. "Neural Mechanisms Of Selective Visual Attention." *Annual Review of Neuroscience* 18, no. 1 (1995): 193-222.
- Druzgal, Tason, and Mark D'Esposito. "Activity in fusiform face area modulated as a function of working memory load." *Cognitive Brain Research* 10, no. 3 (2001): 355-364.
- Ester, E. F., J. T. Serences, and E. Awh. "Spatially Global Representations in Human Primary Visual Cortex during Working Memory Maintenance." *Journal of Neuroscience* 29, no. 48 (2009): 15258-15265.
- Fetz, E. E.. "Operant Conditioning of Cortical Unit Activity." *Science* 163, no. 3870 (1969): 955-958.

- Fetz, E. E., and D. V. Finocchio. "Operant Conditioning of Specific Patterns of Neural and Muscular Activity." *Science* 174, no. 4007 (1971): 431-435.
- Fukuda, Keisuke, Edward Vogel, Ulrich Mayr, and Edward Awh. "Quantity, not quality: the relationship between fluid intelligence and working memory capacity." *Psychonomic Bulletin & Review* 17, no. 5 (2010): 673-679.
- Fukuda, Keisuke, Edward Awh, and Edward K Vogel. "Discrete capacity limits in visual working memory." *Current Opinion in Neurobiology* 20, no. 2 (2010): 177-182.
- Garcia, Javier O., Ramesh Srinivasan, and John T. Serences. "Near-Real-Time Feature-Selective Modulations in Human Cortex." *Current Biology* 23, no. 6 (2013): 515-522.
- Haas, L F. "Hans Berger (1873-1941), Richard Caton (1842-1926), and electroencephalography." *Journal of Neurology, Neurosurgery & Psychiatry* 74, no. 1 (2003): 9-9.
- Harrison, Stephenie A., and Frank Tong. "Decoding reveals the contents of visual working memory in early visual areas." *Nature* 458, no. 7238 (2009): 632-635.
- Hollingworth, Andrew. "Scene and Position Specificity in Visual Memory for Objects.." *Journal of Experimental Psychology: Learning, Memory, and Cognition* 32, no. 1 (2006): 58-69.
- Hollingworth, Andrew. "Object-position binding in visual memory for natural scenes and object arrays.." *Journal of Experimental Psychology: Human Perception and Performance* 33, no. 1 (2007): 31-47.
- Hubel, DH; Wiesel, TN. "Receptive Fields, Binocular Interaction and Functional Architecture in the Cat's Visual Cortex". *Journal of Physiology* 160(1962): 106-154.
- Lepsien, J., and A. C. Nobre. "Attentional Modulation of Object Representations in Working Memory." *Cerebral Cortex* 17, no. 9 (2006): 2072-2083.
- Luck, SJ, and EK Vogel. "the capacity of visual working memory for features and conjunctions." *Nature* 390 (1997): 279-281.
- Miller, EK, L Li, and R Desimone. "Activity of neurons in anterior inferior temporal cortex during a short-term memory task.." *Journal of Neuroscience* 13 (1993): 1460-1478.
- Paradiso, M. A.. "A theory for the use of visual orientation information which exploits the columnar structure of striate cortex." *Biological Cybernetics* 58, no. 1 (1988): 35-49.

- Pasternak, Tatiana, and Mark W. Greenlee. "Working memory in primate sensory systems." *Nature Reviews Neuroscience* 6, no. 2 (2005): 97-107.
- Payne, Lisa, Sylvia Guillory, and Robert Sekuler. "Attention-modulated Alpha band Oscillations Protect against Intrusion of Irrelevant Information." *Journal of Cognitive Neuroscience* 25, no. 9 (2013): 1463-1476.
- Pelli, Denis G.. "The VideoToolbox Software For Visual Psychophysics: Transforming Numbers Into Movies." *Spatial Vision* 10, no. 4 (1997): 437-442.
- Ranganath, C., M.X. Cohen, C. Dam, and M. D'Esposito. "Inferior Temporal, Prefrontal, and Hippocampal Contributions to Visual Working Memory Maintenance and Associative Memory Retrieval." *Journal of Neuroscience* 24, no. 16 (2004): 3917-3925.
- Reynolds, John H., and Robert Desimone. "The Role of Neural Mechanisms of Attention in Solving the Binding Problem." *Neuron* 24, no. 1 (1999): 19-29.
- Riggall, A.C., and B.R. Postle. "The relationship between working memory storage and elevated activity as measure with functional magnetic resonance imaging.." *Journal of Neuroscience* 32 (2012): 12990-12998.
- Serences, J, S Saproo, M Scolari, T Ho, and T Muftuler. "Estimating the influence of attention on population response profiles." *NeuroImage* 44, no. 1 (2009): 223-231.
- Serences, John T., Edward F. Ester, Edward K. Vogel, and Edward Awh. "Stimulus-Specific Delay Activity in Human Primary Visual Cortex." *Psychological Science* 20, no. 2 (2009): 207-214.
- Shadlen, M.N., K.H. Britten, W.T. Newsome, and J.A. Movshon. "A computational analysis of the relationship between neuronal and behavioral responses to visual motion." *Journal of Neuroscience* 16 (1996): 1486-1510.
- Super, H., H. Spekreijse, and VAF Lemme. "A Neural Correlate of Working Memory in the Monkey Primary Visual Cortex." *Science* 293, no. 5527 (2001): 120-124.
- Tsotsos, John K.. "Limited Capacity of Any Realizable Perceptual System Is a Sufficient Reason for Attentive Behavior." *Consciousness and Cognition* 6, no. 2-3 (1997): 429-436.
- Vogel, E K, A W McCollough, and M G Machizawa. "Neural measures reveal individual differences in controlling access to visual working memory." *Nature* 438 (2005): 500-503.
- Zaksas, D, JW Bisley, and T Pasternak. "Motion information is spatially localized in a visual working-memory task." *Journal of Neurophysiology* 86 (2001): 912-921.