

THE CONTRIBUTION OF ALPHA OSCILLATIONS TO
WORKING MEMORY PROCESSING

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THESIS ABSTRACT

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Working memory, which enables the temporary storage of information in an active “online” state, is an exceptionally capacity limited system. Given this capacity limit, irrelevant information in our environment must be filtered out, while relevant representations are maintained. Research has shown that neural oscillations in the alpha frequency range (8-12Hz) are greatly influenced by the number of items in memory. Most work has argued that alpha oscillations primarily support working memory processing by suppressing information that could interfere with items already in memory, as indexed by an increase in alpha power. However, other work has shown that decreases in alpha power, with little evidence of concurrent increases, support the maintenance of working memory representations.

In this thesis we show that, in the context of visual working memory, the primary role of alpha oscillations is to maintain distinct working memory representations, rather than to suppress irrelevant information. This is shown in a series of three experiments all indicating that as the number of relevant items increases, the power of alpha oscillations systematically decreases. In the first experiment, we use a whole report and change detection task to examine how the number of items in memory influences alpha oscillations. In the second experiment,

we use a cuing (Experiment 2A) and filtering (Experiment 2B) paradigm to demonstrate that alpha power tracks the number of remembered items instead of the number of total items on the screen. Lastly, by presenting items sequentially (Experiment 3A) or in overlapping locations (Experiment 3B), we see evidence that decreases in alpha power are related to the maintenance of relevant spatial locations, instead of the number of items in memory. The results of the experiments suggest that alpha power reflects the maintenance of relevant working memory representations, rather than the suppression of irrelevant external distractors or the inhibition of task-irrelevant neural areas. Furthermore, our last experiment indicates that the alpha frequency band is especially sensitive to the maintenance of spatial information.

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To my parents, Luljeta and Pllumb Maçe, who taught me the value of education, hard work, and following through. Without their guidance I would be lost.

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CHAPTER I

INTRODUCTION

The oscillatory dynamics of neuronal circuits are well known to be important to behavior (Buschman et al., 2012; Jutras & Buffalo, 2014; Thut, Miniussi, & Gross, 2012). For example, oscillatory activity of neuronal populations are a well characterized signature of various stages of sleep, and are often found to be atypical in individuals with clinical disorders such as epilepsy or Parkinsons disease (Kühn et al., 2005; Ren et al., 2015). A prominent theory for why oscillations exist is that neurons form functional networks that are based on synchronized firing (Cohen, 2014; Engel, Fries, & Singer, 2001; Fell & Axmacher, 2001). The oscillations that we observe using scalp electroencephalography/magnetoencephalography (EEG/MEG) recordings reflect the fluctuations in post-synaptic potentials of excitatory and inhibitory neurons. Furthermore, only a relatively small number, about two percent of neurons in 1 cm of cortex, need to fire synchronously for an oscillatory pattern to be observable on the scalp (Shaw, 2003). In this paper we will concentrate on alpha-frequency oscillations, and the role they play in higher order cognitive processing, particularly in visual working memory processing.

Although the general gist of a complex environment can be obtained rather quickly (Potter, 1976), the detailed encoding and representation of items that compose the environment requires that we continuously fixate on objects of interest. Importantly, object representations quickly fade as our eyes move and

fixate on new items (Irwin, 1992). Consequently, we need a visual memory system that is able to maintain the detailed representations that we want to hold onto for the particular task at hand. This ability is referred to as visual working memory (VWM). In the Baddeley and Hitch model of the working memory system, visual working memory is subject to the same capacity constraints as verbal information (Baddeley, 2003). That is, this system is limited in the amount of information that may be maintained, manipulated, and later compared. In the following sections, we review the work relating synchronized neural firing to higher level cognition, then we outline work relating neural oscillations with the capacity limits of working memory. Lastly we concentrate on alpha oscillations and their purported role in VWM processing.

The Role of Neural Oscillations in Cognitive Processing

Since the discovery of EEG activity by Hans Berger, a swath of research has shown that the brain has networks of neurons that fire in synchrony. Furthermore, these oscillations vary by mental state; for example, when individuals are relaxed, the EEG shows an increase in the prevalence of lower frequency oscillations, such as in the delta (<4Hz) to alpha (7.5Hz-14Hz) frequency ranges (Shaw, 2003). However, when individuals are performing a cognitively engaging task, such as difficult recall or match-to-sample tasks, neural regions recruited to perform the task begin to produce higher frequency oscillations, typically in the beta (14-30Hz) to gamma (30Hz+) frequency ranges (Bauer et al., 2014; Fries et al., 2001; Honkanen, et al., 2014; Jensen, Kaiser, Lachaux, 2007; Roux et al., 2012). Though these relationships

between oscillations and behavioral states have been well documented, the exact function of neural oscillations in behavioral performance is a relatively new topic of research.

Until the work of Wolf Singer and Charles Gray there was relatively little work describing the functional role that neuronal oscillations in communication between neural populations (Gray & Singer, 1989; Singer & Gray, 1995). One key observation made by Singer and Grey (1995) was that neuronal signals are much more effectively propagated when multiple neurons fire in unison rather than asynchronously. That is, for a signal that needs to be communicated between two separate cortical areas, the likelihood of the signal being effectively passed along is much higher if neurons coding for the same information fire together rather than separately. The synchronized firing of neurons has also been proposed to be the mechanism through which working memory representations are actively maintained. For example, Compte et al. (2000) proposed a model of working memory for spatial location in which peaks of activation within neuron networks in the prefrontal cortex represent each location. In this model, the neurons that code for similar locations are linked through recurrent excitatory connections, and the strength of this excitatory coupling decreases as a function of preferred location. Furthermore, lateral inhibition between neurons preferring different locations leads to a type of “bump” attractor model of memory that is able to sustain representations without recurrent external input (Rao et al, 1999). Though the bump-attractor model has been supported by much computational and physiological research (Wang et al., 2004; Wimmer et al., 2014), one question that

has still remained is how these representations are formed or extinguished. This question leads us back to the role of alpha oscillations.

One proposed function for neural oscillations is that they reflect physiological processes that underlie different types of cognitive functioning. For example, a recent model by Dipooa and Gutkin (2013) proposes that different types of neural oscillations reflect different mechanisms of processing. Within this model, beta/gamma frequency oscillations reflect the selection of relevant representations; theta frequency oscillations reflect the active maintenance of relevant information, while the rapid clearing of irrelevant distractors is reflected in alpha oscillations. This inhibition account of alpha oscillations has become the dominant theory of the role of alpha frequency oscillations in recent years and will be the focus of the current experiments. However, before delving into the specific role of alpha oscillations, we should outline how neural oscillations may be the basis of the limits of working memory.

One striking feature of working memory is its severe capacity limit. Recent models of memory based on neural oscillations may provide a reason for this severe capacity limit. Provided that items in memory are coded via synchronized firing of neural assemblies, one question that remains is how we are able to maintain more than one representation concurrently. One theory by Lisman and Idiart (1995) proposes that multiple representations are maintained by forming multiple assemblies which fire slightly out of phase with one another. That is, neurons that code for one representation have bursts of synchronized firing at a particular high frequency (typically high-beta-low gamma), that occur at specific phases of lower

frequency oscillation. Thus, by separating the burst of high-frequency representations into different phases of the lower-frequency oscillation, multiple representations can be maintained concurrently.

There are several predictions that this type of coding scheme makes. First, the sequential nature of coding sets a natural pattern to how the representations are coded and later recalled. Second, the phase-space of the lower-frequency oscillation limits the number of representations that may be maintained, since there are only a limited number of high frequency bursts that can occur within one phase cycle of the lower frequency representation. Both of these predictions have been supported by empirical evidence. The first prediction is well supported by findings of a sequential read out of representations. For example, when individuals are given lists of words to remember, then later recall whether a test item was part of the original set, reaction times systematically increase as the list of items increases, suggesting the items are serially scanned until the target probe is identified (Jensen & Lisman, 1998).

The second prediction has been supported by recent findings using both humans and non-human primates. Miller and colleagues found that when monkeys hold multiple images in memory over a short-delay period, neurons in the prefrontal cortex encoded information about each object at different phases of an ongoing (32Hz) oscillation. A striking demonstration of the importance of this phase coding was evident in their error trials; when the monkeys misremembered the order of time presented items, there was a significant decrease in the phase separation between the two representations. Expanding on these findings,

Axmacher and colleagues (2010) recorded inter-cranial EEG from clinical populations to show that an increase in the number of remembered items, leads to a shift in the dominant lower-frequency oscillation. As individuals had to remember more items, there was a shift in theta oscillation towards lower frequencies; this suggests that an increase in the phase space of the dominant lower frequency could help accommodate more items in memory.

The research outlined above indicates that neural oscillations may provide a clue on the reasons underlying our severely limited short term memory. That is, phase-coding models necessitate a capacity limit because only a limited number of representations can fit within one oscillatory cycle. Once those limits are reached, items are either prohibited from entering memory, or representations may be extinguished because a necessary level of separation/individuation is exceeded. Consequently, an important aspect of memory is the exclusion of extraneous representations once capacity has been reached. This important function has been associated with alpha-frequency oscillations.

Alpha Oscillations and Their Relation to Attention and Memory

Alpha oscillations are one of the most dominant rhythms exhibited by the human cortex. These oscillations, which can emerge from communication within thalamo-cortical networks (Suffczynski et al., 2001), are thought to reflect mechanisms of inhibitory control (Klimesch et al., 2007). Studies of both attentional processing and working memory have argued that alpha power increases reflect

sensory gating of irrelevant information through the disengagement of task-irrelevant brain regions (Jensen and Mazaheri, 2007). In studies of attentional processing, participants are given difficult detection tasks, and asked about the presence of a particular target item. The results typically show that when pre-stimulus alpha power is high, the probability of detecting the target is significantly lower than when pre-stimulus alpha power is low (Banerjee et al., 2011; Bauer et al., 2014; Bonnefond & Jensen, 2012; Bush, Dubois, & VanRullen, 2009; Kelly et al., 2006). Furthermore, in tasks that employ a lateralized design, such that one half of the visual field must be ignored while one half must be attended, participants are typically much more accurate at detecting a target item when the asymmetry in alpha power between the attended and unattended hemifields is higher. Namely, when alpha power over the hemisphere representing the unattended (distractor) side is much higher than alpha power over the hemisphere representing the attended side, the detection of target items is typically much higher than when the power is more comparable (Foxye & Snyder, 2011; Handel, Haarmeier, & Jensen, 2011).

Additional studies have also shown that the reverse is also true. When there is a substantial decrease of alpha power relative to a pre-trial baseline period, detection rates are typically higher and reaction times are faster (Hanslmayr et al., 2007; Rohenkohl & Nobre, 2011; Snyder & Foxye, 2010; vanDijk et al., 2008; Yamagishi, et al., 2008;). These different levels of alpha synchronization/desynchronization are thought to reflect two different mechanisms (Rihs, Michel, & Thut, 2009. The increase in synchronization from a pre-stimulus

baseline to post-stimulus processing is thought to reflect a reduced state of active information processing in task-relevant neuronal networks. In contrast, the desynchronization of alpha-band activity has been interpreted to reflect an increased excitability of neurons, and thought to lead to increased information transfer between thalamo-cortical networks (Pfurtscheller, 1992; Pfurtscheller & Lopes da Silva, 2005).

Though the majority of studies examining the relationship between alpha power and behavior employs sensory perceptual or attention tasks, there is also a number of studies examining how alpha relates to working memory ability. A paradigm that has often been used in this research is the modified Sternberg task. In this task, individuals are given sets of alpha-numeric characters to memorize. To avoid sequence effects introduced by a serial presentation of items, the letters are often presented simultaneously, and set-size is manipulated by adding more or less relevant items in the display. To avoid the visual discrepancies between set-sizes, irrelevant Xs are typically added as flankers in the display, thereby manipulating the memory load while keeping the number of items in the display the constant (Jensen et al., 2002; Klimesch et al. 1997). Using this task paradigm, Klimesch and colleagues have observed that higher alpha power, indicative of increased synchronization, is often associated with more accurate recall of items in the memory set (Klimesch, et al., 1999). This overall increase in alpha power has been interpreted as a mechanism for inhibiting neural areas that could interfere with the task at hand, or as a mechanism of inhibiting sensory areas from assimilating additional extraneous information (Neupert & Pfurtscheller, 2001; Pfurtscheller, 1992, 2001).

Furthermore, these studies have shown that higher memory array set-sizes typically elicit greater increases in observed alpha power (relative to baseline power). The set-size dependent increase has been interpreted as reflecting increased inhibition of task-irrelevant areas. In other words, the more difficult the task becomes, the more necessary it becomes to inhibit task-irrelevant brain regions that could interfere with the increasingly difficult task (Klimesch, 1999; Klimesch, Sauseng, & Hanslmayr, 2007).

This brings up an important distinction between what memory studies and those in the perception/attention literature regard as signals that characterize successful performance. In the perception/attention literature, higher alpha power is thought to reflect the successful inhibition of task-irrelevant information from ever being processed, indicative of the 'gating' mechanisms that alpha-frequency oscillations reflect. Additionally, greater desynchronization is related to the successful detection and processing of target items (Ergenoglu, et al., 2004; vanDijk et al., 2008), possibly indicating an open 'gate' for information to be processed. However, this is where the results of work on perceptual/attention processing begin to diverge from the conclusions of studies on working memory processing. While both studies on perception and studies on memory seem to agree that alpha synchronization is beneficial to task performance, they do not seem to converge on a similar conclusion about the role of alpha desynchronization. In the perceptual literature, desynchronization has been shown to reflect the successful encoding of relevant information. However, in the working memory literature, alpha desynchronization is often either not observed or thought to play a smaller role in

the successful representation of items in memory (Palva et al., 2011).

One of the central goals of the current research is to examine this discrepancy over the role of alpha desynchronization in the literature, especially within the context of VWM. One reason for focusing on VWM is that studies on alpha activity and working memory have typically used tasks that require some level of verbal processing (Jensen et al., 2002; though see also Medendorp et al., 2007; Palva et al., 2010, 2011). The use of verbal stimuli to examine alpha power fluctuation is especially problematic if alpha is sensitive to semantic demands. For example, Klimesch et al. have observed differences in synchronization/desynchronization of alpha that has been subdivided into different sub-bands. In this procedure, alpha is partitioned into one or two lower-alpha bands, and an upper alpha band, each with a frequency range of about 2Hz from an individual's peak alpha frequency (the frequency within the alpha band showing the greatest power). This procedure is supposed to be a better method of measuring changes in alpha frequency, as the two sub-bands could reflect two substantially different cognitive mechanisms (Klimesch et al., 1999). According to this theory, desynchronization in the lower alpha band (~2Hz below peak alpha power) is likely to reflect basic task demands such as arousal and task engagement; while the upper alpha desynchronization is more likely to reflect task requirements that are distinct to the task at hand, such as semantic or memory processing (Doppelmayr et al., 2002; Klimesch, Vogt, & Doppelmayr, 1999). This sensitivity to the type of task that participants are performing makes it especially problematic to extrapolate the role of alpha oscillations in VWM processing from research using verbal or phonetically encoded

items (Bonnefond, & Jensen 2012; Jensen et al., 2002; Klimesch et al., 1999; Klimesch, Schimke, & Schwaiger, 1994).

The few studies that have more directly examined the role of working memory processing using a VWM task have either primarily focused on alpha phase synchronization (Palva et al., 2010) or see varying levels of synchronization/desynchronization depending on the cortical area of interest (Palva et al., 2011). The work of Palva et al. (2011) hints at differences in the role that alpha plays in visuospatial versus verbal memory tasks. Using a Luck and Vogel (1997) change detection paradigm, the authors found that alpha-frequency oscillations were suppressed below baseline levels following the memory set. Furthermore, changes in alpha power, especially in occipital/occipito-temporal regions, were negatively correlated with memory load. That is, there was a greater reduction in alpha power with increasing memory load. These findings are the opposite of what would be predicted by the inhibition hypothesis (Klimesch et al. 2007) and directly contradict the findings of Jensen and colleagues (2002).

Another indication that the inhibition hypothesis may not be as straightforward as has been previously thought comes from studies manipulating task difficulty. Recall that according to the inhibition hypothesis, greater synchronization of alpha is observed under the most difficult task conditions because 'gating' against irrelevant information (external or internal) is especially necessary during hard tasks. However, the opposite pattern of results has also been shown. For example, Gevins and colleagues have shown an increase in alpha power

as task difficulty increases in both verbal and spatial versions of n-back task (Gevins, Smith, McEvoy, & Yu, 1997; Gevins & Smith, 2000; McEvoy, Smith, Gevins, 1998).

One potential difference between these two studies is the way that the alpha oscillations are being analyzed. For example, in the first, Klimesch et al., (1999), parsed alpha into lower and upper frequencies, while the Gevins' studies did not bifurcate the alpha band. As alluded to earlier, Klimesch argues that this division is necessary for being able to detect the specific mechanisms reflected in alpha activity.

In all, current research on alpha-frequency oscillations suggests that levels of desynchronization and synchronization during performance of a cognitive task reflect task demands. Given the inconsistency in the findings relating alpha-signals to working memory processing, the present experiments examine how changes in alpha oscillations are related to VWM encoding and maintenance demands. To this end, multiple versions of a visual working memory task were adopted. These tasks had varying levels of memory demands and distractor suppression. By examining these different task designs, we expect that our findings further elucidate the meaning of EEG alpha oscillations to cognitive processing, and particularly their role in VWM processing.

CHAPTER II:

ALPHA POWER IN A VISUAL WORKING MEMORY TASK

Introduction

Given the discrepancy in the literature over the role of alpha-frequency oscillations, the aim of the first experiment was to examine the pattern of alpha-frequency oscillations in VWM task. We examined alpha-frequency oscillations both under a typical change detection (CD) task (Luck & Vogel, 1997) and whole-report task (Adam et al., 2015). Since the experiments of Luck and Vogel (1999), many studies have used the CD task to estimate VWM capacity. However, as mentioned above, very few studies have used this task to estimate the role of alpha oscillations in memory. Thus, a critical aim of the first experiment was to examine how alpha-frequency oscillations track performance on a widely used VWM task.

In addition to CD, we used a whole-report task to more precisely estimate how VWM capacity fluctuates on a trial-by-trial basis, and whether fluctuations in capacity can be captured by variations in alpha power. Though the change detection simplifies the observers' decision during the response stage (Rensink, 2002), the task does not allow us to estimate the observers' capacity on a trial-by-trial basis. Thus, since we wanted to examine how alpha-oscillatory signals track both set-size and accuracy during every trial, we also ran a whole-report procedure. Recent studies from our lab have validated that performance in the whole-report procedure is highly correlated to CD performance, and the measure has very high internal reliability (Adam et al., 2015).

There are several advantages to using these two working memory measures.

First, the use of color-shapes instead of letter/number stimuli minimizes the use of semantic coding, yielding a better estimate of memory processing without the potential use of phonological rehearsal. Second, the whole-report procedure affords a better estimate of working memory load under the most difficult task procedures. Klimesch et al. (1999) manipulated difficulty by having participants remember either 5 or 10 letters/numbers in a 'varied' or 'consistent' mapping conditions. In the 'consistent' mapping condition, the memory set items were repeated over the course of 10 trials; while in the 'varied' condition, memory-sets changed on every trial. Based on the result that the 'varied' set-size 10 condition yielded the lowest accuracy and highest increase in alpha power, the authors concluded that alpha synchronization increases with difficulty. However, one potential problem with this finding is that it is difficult to determine exactly how many items individuals were representing during every trial. With a 50/50 chance accuracy, it could be that participants were guessing on a good proportion of trials. This leaves the possibility that in the most difficult condition, in which the guessing rate is likely the highest, the increase in alpha-synchronization is related to the failure of maintaining much of the memory set. Though this is speculative, the whole-report procedure allows us to examine how memory failures are related to alpha power on a trial-by-trial basis.

To maximize the possibility of finding similar results to studies endorsing the inhibition hypothesis, we analyzed the alpha-frequency data in several ways. First, we wanted to examine the signal without baselining or transforming the data into an event-related desynchronization/synchronization (ERD/ERS) signal, as is often done by Klimesch and colleagues (Klimesch, et al., 1997; Klimesch et al., 1998;

Klimesch, Schimke, Schwaiger, 1994; Pfurtscheller, & daSilva, 1999). We had two main reasons for not wanting to transform the data: First, we wanted to examine how the pre-trial baseline activity relates to performance on both the CD and whole-report tasks, and second, the conversion into a percent signal change (as is done in the ERD/ERS method) can obfuscate subtle differences in power across set-size conditions and tasks. That is, though the ERD/ERS method gives a reliable estimate of how retention-period activity changes relative to the baseline period, it does so at the cost of eliminating usable information from the baseline period. Thus, for our first analysis of the data, we examine only the raw alpha-power.

Our second analysis more closely resembles previously used methods of measuring changes in alpha power (Klimesch, et al., 1998; 1999). Here, we first determined each individual's peak alpha frequency. The individual alpha frequency (IAF) method has been said to produce more reliable estimates of alpha power because lower and upper alpha bands may reflect drastically different processing mechanisms. For example, Klimesch et al. (1997) used a verbal working memory task to show that upper alpha frequency synchronization is related to more accurate subsequent recall of the memory items, while desynchronization in the lower alpha band was associated with more accurate subsequent recall.

In all, the goals of our first experiment were twofold. First, we wanted to examine the patterns of alpha-frequency oscillations while participants are performing a widely used and well validated working memory task. Second, we wanted to examine how our results support what has already been observed in the literature.

Experiment 1: Change Detection and Whole-Report

Methods

Participants

38 young adults (18-35 years old) participated in this study. Due to an insufficient number of trials, 4 participants were excluded from the grand analysis (exclusion criteria are outlined below). The final sample comprised of 34 participants. All participants had corrected-to-normal vision and reported no current or history of mental/psychological disorders. Participants gave written informed consent prior to the experimental session. The experimental procedures were approved by the University of Oregon's Committee for the Protection of Human Subjects (CPHS) and Institutional Review Board (IRB). Subjects that had rejection rates that exceeded 25% of trials were excluded from the grand analysis (rejection procedures are outlined below). This resulted in a total of 4 subjects being excluded, leaving a total of 34 subjects in the analysis sample.

Experimental Tasks

Participants performed a CD and whole-report VWM task; see Figure 1. The two tasks were blocked; all participants performed the whole-report task first, followed by the CD task. Participants initiated each trial by pressing the spacebar on a computer keyboard. Following a 1300ms baseline period, participants were shown either 1, 2, 3 or 6, highly discriminable colored squares on a grey background. The memory set items were shown for 150ms and followed by a 1150ms retention period (see Figure 1). The memory sets were chosen at random from the following colors: red, blue, green, cyan, magenta, yellow, white, black.

Repetitions of colors were not allowed.

In the change detection blocks, participants used a keyboard response to indicate whether they detected that the single item (“probe”) item had or had not changed. In the whole-report blocks, participants were instructed to use the mouse to click on the response-pads to indicate the color for each item in the memorandum. Participants were encouraged to respond to as many colors as possible, but they could use the spacebar to initiate the next trial if they felt as though they could not remember any more colors. Participants performed 4 blocks of 96 trials in the CD task, and 5 blocks of 96 trials of the whole-report task. In the whole-report task participants performed a total of 80 trials of set-sizes 1-3, and 240 trials of set-size 6. We chose to have participants perform a greater number of set-size 6 trials because we anticipated that this set-size would give us the greatest variability in performance, and would also allow us to examine the neural signatures performance failures. In the CD task, participants performed a total of 96 trials per set-size.

Data Acquisition and Analysis

EEG data was recorded using an SA Instrumentation amplifier with a bandpass of 0.01-80Hz, and digitized at 250Hz using LabView software. Data was recorded using tin electrodes mounted on an electrode cap (Electrocap International) according to the International 10-20 system with 4 additional sites: OL and OR, positioned midway between O1 and T5 on the left hemisphere and O2 and T6 on the right hemisphere; POz, located on the midline between Pz and O1-O2, and PO3 and PO4, located halfway between POz and T5 on the left and POz and T6 on the right. All

sites were record using a left-mastoid reference, and right-mastoid ground.

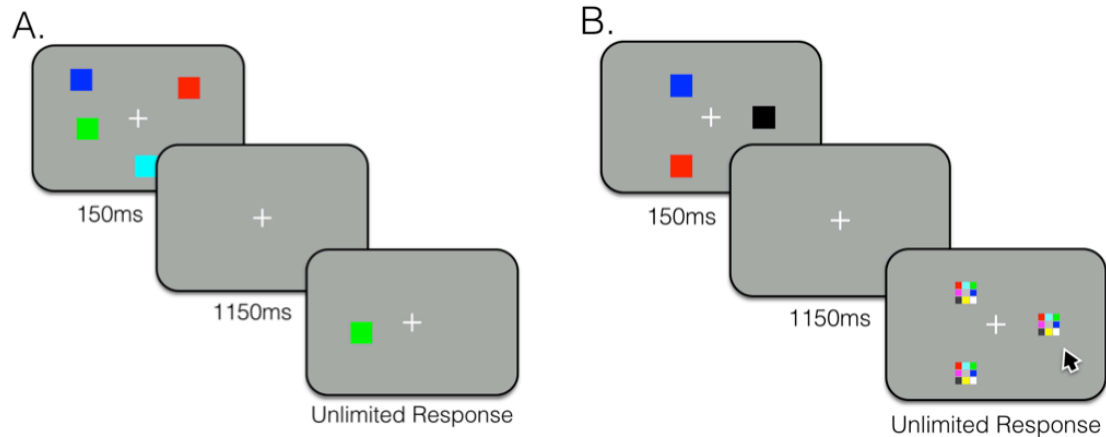


Figure 1: Tasks used in Experiment 1. A) Change detection task adopted after Luck and Vogel (1997). B) Whole report procedure: stimuli and timing were similar to the change detection task, with the exception that individuals were asked to report all stimuli they remembered from the memory array.

The horizontal electrooculogram (EOG) was recorded from electrodes placed approximately 1cm to the left and right from the external canthi of each eye. The vertical EOG was recorded from an electrode placed 1cm beneath the right eye and referenced to the left-mastoid. Electrode impedance did not exceed 3 k Ω . Trials that contained any artifacts (amplifier blocking, ocular movements or blinks) were excluded from further analysis.

Estimation of EEG Power

First, we computed instantaneous band power by using a Hilbert transform of the EEG signal; the spectral power was band-pass filtered according to the conventional

frequency band of 8Hz to 12Hz for the Alpha band using a two-way least-squares FIR filter (using the eegfilt.m function from EEGLab; Delorme & Makeig, 2004). The instantaneous amplitude of the complex-valued analytic signal was then extracted using a Hilbert transformation; we squared the amplitude signal to estimate power. These power-estimate were used in our first analysis of unbaselined power.

In the second analysis we tailored each participant's alpha frequency band using the individualized alpha frequency (IAF) method defined in Klimesch et al. (1999). For each subject, we first estimated the mean peak frequency within the alpha band (pA) across all electrodes and trials during the baseline period of both the CD and whole-report tasks. This mean value was then used as an anchor point to define 3 different frequency bands with a bandwidth of 2Hz: lower alpha-1 (pA-4 to pA-2), lower alpha-2 (pA-2 to pA), and upper alpha (pA to pA+2).

To estimate how the alpha power changed after the memory array onset, we estimated the event-related synchronization/desynchronization (ERS/ERD) change in power relative to baseline . This was done using the same methods outlined by Pfurtscheller and Aranibar (1977) and used in Klimesch et al (1998). First, we calculated alpha-band power based on the IAF analysis outlined above. We then averaged across conditions/trials; then, for each participant, we calculated ERS/ERD by subtracting the baseline power from the retention period power for each electrode channel according to the following equation:

$$\text{ERS/ERD} = \frac{\text{Power}(\text{memory}) - \text{Power}(\text{baseline})}{\text{Power}(\text{baseline})} \times 100\%.$$

Thus, based on this equation ERS is defined as a positive increase during the memory period, and ERD is defined by negative values between a baseline and memory period. We used a 1 second baseline period from -1200ms to -200ms before the presentation of the memory array to avoid any effects related to the participants' anticipation of the memory array items. This baselining analysis was only applied to the IAF power data.

Statistical Analysis

We derived VWM capacity (K) estimates in the CD task using the formula first outlined by Cowan (2001): $K = \text{set-size} * (\text{hits} - \text{false alarms})$, where K represents the number of objects sorted, set-size is the number of items in the memory set, hits are the correctly detected changes, and false alarm are the proportion of "same" trials in which the participant said "different". In order not to artificially underestimate capacity, we only used at or above capacity trials (set-size 3 and 6) to estimate K.

In the whole-report task, we estimated capacity as the average number of correctly identified items on set-size 3 and 6 trials. Furthermore, we estimated the proportion of trials in which participants exhibited both complete and partial lapses (in set-size 3 and 6 trials) and good performance. Complete lapses were defined as trials in which participants got 0 or 1 items correct, partial lapses were defined as trials in which the participants responded to 2 or fewer items correct. Good performance trials were defined as trials in which the participants got 3 or more items correct (Adam et al., 2015).

The significance of the unbaselined and baselined ERS/ERD effects was

assessed first by a repeated measures analysis of variance (ANOVA) with condition, time interest, and frequency (for the ERS/ERD analysis) as factors. Whenever Mauchley's test sphericity was violated, we used Greenhouse-Geisser corrected value. Post-hoc analysis of main effects and interactions were assessed through paired two-way t-tests. Alpha levels were adjusted with a step-wise Bonferroni correction to control for multiple comparisons to yield an overall $p < .05$; however for some analyses, unadjusted values are also reported (see Note 1 and 2). To reduce the number of comparisons, we binned data into ~ 250 ms (236ms) time bins; for a total of 11 time bins per trial; 5 of which correspond to the retention-period activity. We discarded the first and last time bins from our analysis because of the edge effects introduced by band-pass filtering the data; this left us with 4 retention-period time bins (120ms to 1064ms). Baseline power was averaged from -1000ms to -200ms pre-memory array. When relevant, we pooled across frontal and posterior channels; frontal channels consisted of: F3, F4 and Fz; posterior channels consisted of electrode sites: PO3/PO4, T5/T6, OL/OR, O1/O2, and POz.

Results

Behavioral Results

The mean VWM capacity estimate in the CD task was 2.94 items (SD=0.64; range: [1.62, 4.17]). The mean whole-report estimate was 2.62 (SD=0.40, range:[1.93, 3.44]). Similar to previous studies in our lab (Adam et al., 2015), we found a strong positive relationship between CD and whole-report performance ($r=0.67$, $p < .01$, 95% Confidence Interval (CI): [0.44 0.82]), see Figure 2A. We saw a

strong negative relationship between change detection performance and both complete attentional lapses ($r=-0.61, p<.01, CI: [-0.35 -0.79]$) and partial lapses ($r=-0.62, p<.01, CI: [-0.36 -0.79]$).

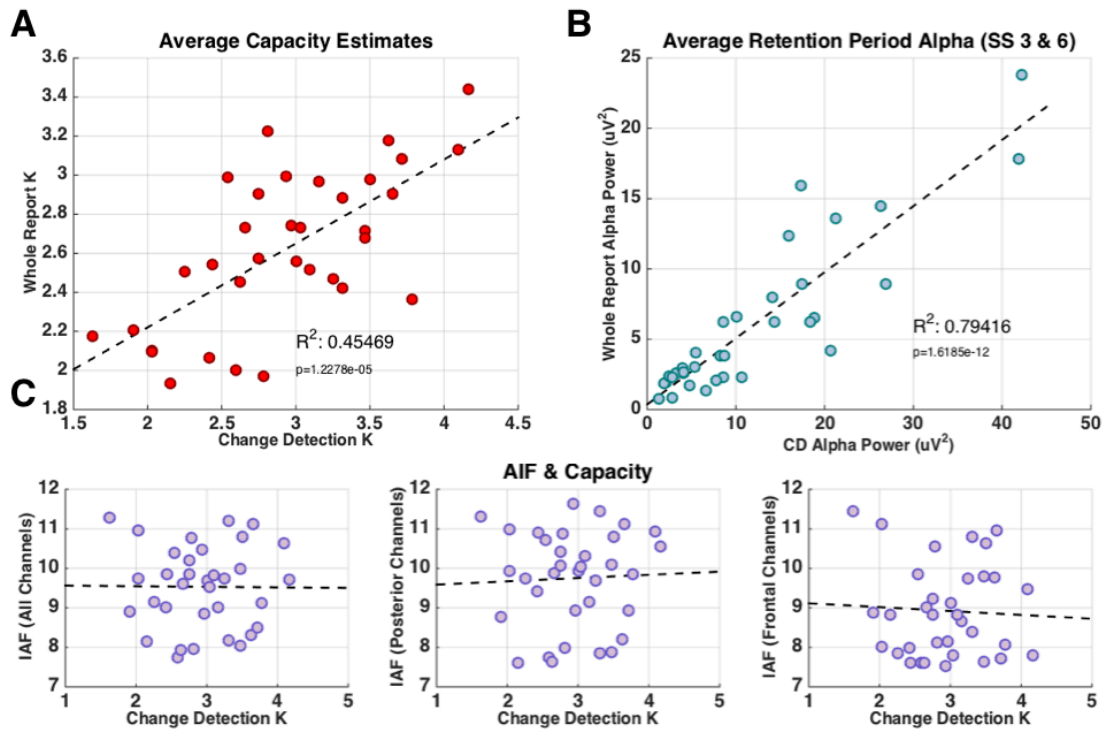


Figure 2: A) Correlation between change detection and whole report performance. B) Correlation between average retention period (120ms-1064ms) alpha power in the CD and WR task for set-sizes 3 and 6. C) Correlations between IAF estimates (using all, posterior, and frontal electrodes) and CD capacity.

EEG Results

Broad-band power for all estimated frequencies is shown in Figure 3. As is apparent in the figure, posterior electrodes showed a high level of alpha power.

Change Detection Data

The unbaselined alpha activity for the change detection task is shown in Figure 4A. A repeated measures ANOVA revealed a significant main effect of condition

($F(2.10,69.26)=4.86, p<.05$), and time ($F(1.46,48.16)=16.75, p<.01$); and a significant interaction between condition and time ($F(4.14,136.51)=4.09, p<.01$).

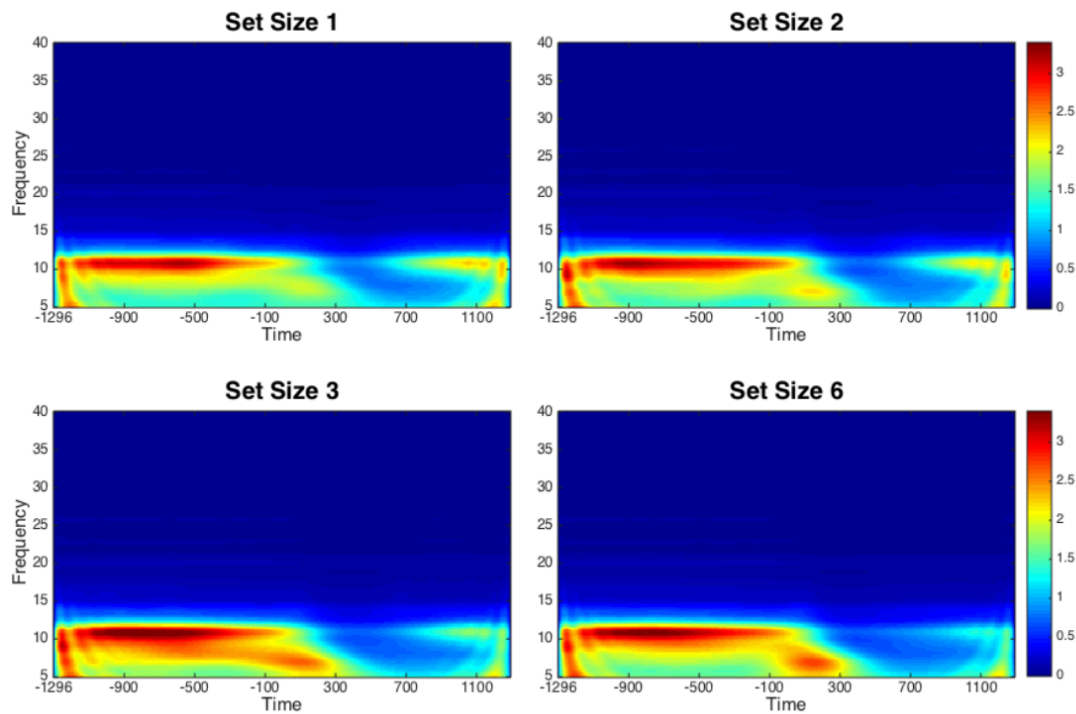


Figure 3: Unbaselined power data. Plots depict average power across posterior electrode sites (an average for both the change detection and whole report tasks). We observed a prominent alpha signal across all set-sizes, which decreased with the onset of the memory array. Towards the end of the trial, alpha level increases, but remains below the baseline levels.

Planned comparisons revealed a significant difference between the set-size 1 and set-size 3 conditions ($t(33)=2.90, p<.04$) and a marginally significant difference between set-size 1 and set-size 6 ($t(33)=2.70, p=0.06$). If we restricted our analysis to just the retention period, we again found a significant difference between set-size 1 versus set-size 2 and set-size 1 versus 3 (all $t(33)>2.99, p<.03$); set-size 3 and set-size 6 were also significant ($t(33)=2.87, p<.05$). Baseline power did not significantly differ between any condition ($F(2.48,81.68)=1.52, p>.20$).

Examining the change in power across time, we found a significant difference between baseline power and all time bins starting from 120ms to the end of the trial (all $t(33) > 3.23$, $p < .05$). Splitting the data by set-size, we found a significant reduction in power for all set-sizes in the 120ms to 826ms interval ($t(33) > 3.95$, $p < 0.01$), however, with the exception of set-size 6 (significant until 1064ms), activity was marginally significant from baseline in the 826ms to 1064ms interval ($t > 2.22$, $p < 0.03†$).

Examining accurate versus inaccurate set-size 3 and set-size 6 trials (combined), we did not find a significant difference between any time bin (all $t(33) < 1.31$, $p > 0.19$).

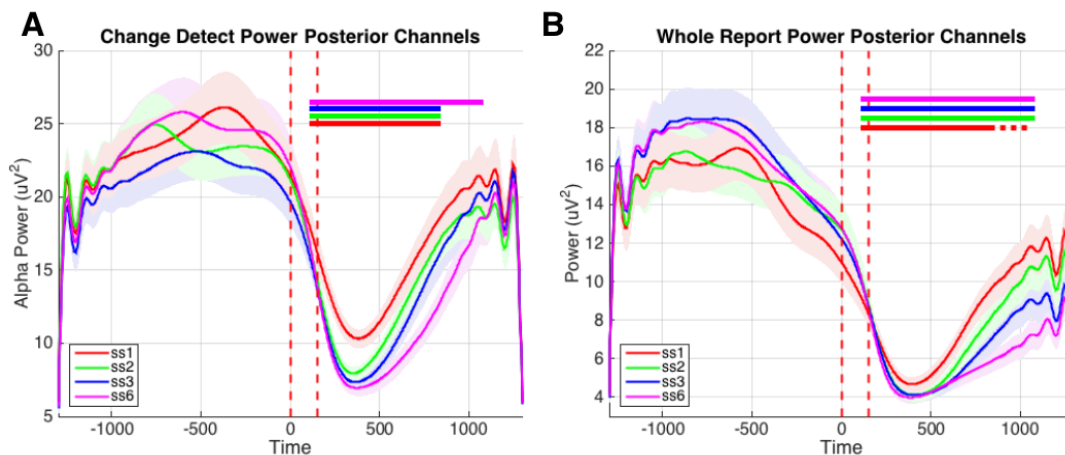


Figure 4: Average unbaselined alpha power observed in A) the change detection and B) the whole report task. Shading represents the standard error of the mean across participants. Colored bars represent significant difference from baseline for each set-size condition. Dotted lines represent a marginally significant difference.

Whole-Report Data

Alpha power in the whole-report task is plotted in Figure 4B. A repeated measures ANOVA with time (baseline to the end of the trial) by condition showed a significant main effect of time ($F(1.35,165)=20.205, p<.01$), but not condition ($F(3,99)=1.31, p>.05$); the interaction was significant ($F(3.62,119.35)=7.87, p<0.01$). However, when we restricted our analysis to just the retention period activity (from 120ms to the end to the trial), we found a significant main effect of condition ($F(1.71, 56,57)=5.97, p<.01$). Baseline activity did not show a significant difference between any of the conditions ($F(2.54,84.08)=2.70, p>.05$).

Activity in the retention period of the whole-report task followed a similar pattern to the CD task. We saw a significant reduction in alpha-power during the retention period (compared to the average baseline) beginning at about 120ms to the end of the trial (pairwise comparisons: all $t(33)>4.30, p<0.001$). When we split the data into conditions we found a significant reduction in power during the retention period relative to baseline for almost all set-sizes (all $t(33)>3.75, p<.001$). The only exception to this pattern was set-size one activity, which failed to reach significance towards the end of the retention period (826ms-1064ms; $t(33)=2.99, p=0.005^*$).

To examine whether power tracks behavioral performance, we combined set-size 3 and set-size 6 trials (see Figure 5). A repeated measures ANOVA on accuracy (low accuracy: partial lapse(0, 1, or 2 correct) and good trials (3 or more correct)) by time (retention period only) revealed a non-significant though trending main effect of accuracy ($F(1,33)=3.44, p=0.07$). When we compared the accuracy data

across time, we found that low accuracy versus good trials primarily differed in the 592ms to 1064ms time interval ($t(33) > 2.16$, $p < 0.04$ *).

We found a strong correlation between retention period (120ms-1064ms) alpha power in the CD and whole-report tasks ($r = 0.85$, $p < .01$, CI: [0.71, 0.92]); see Figure 2B. This pattern was the same when we compared across set-size conditions (all $r > 0.77$, $p < .001$). Despite this strong correlation, retention-period alpha power was significantly lower in the whole-report task than in the CD task (average alpha power across set-sizes: $t(33) = 5.56$, $p < .001$; between set-sizes: all $t(33) > 4.71$, $p < .01$). The same was true for the baseline activity (average baseline power across set-

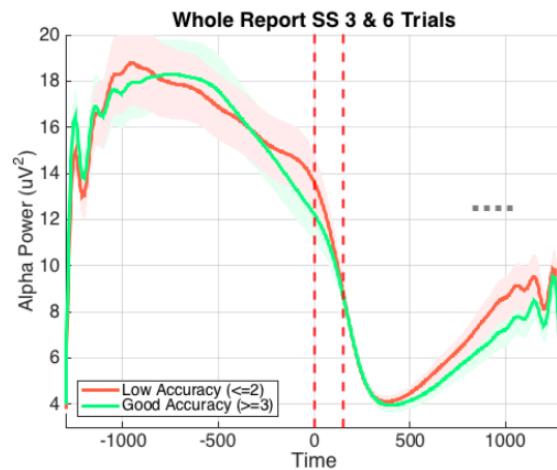


Figure 5: Average power difference between good and bad performance trials in the whole report task (combining across set-size 3 and 6 trials). Shading represents the standard error of the mean; dotted horizontal line represents a marginally significant difference between low accuracy and good accuracy trials.

* The difference is not significant if we adjust for multiple comparisons.

† Some of the time-bins did not survive the adjusted alpha significance level.

sizes: all $t(33)=3.96$, $p<.001$; between set-sizes: all $t(33)>3.05$, $p<.01$); this trend could be explained by participants performing the whole-report task first and CD task second.

ERS/ERD Based on IAF

We failed to find a significant relationship between CD capacity and peak the alpha frequency ($r=-.01$, $p=n.s.$), or whole-report performance and peak alpha frequency ($r=0.08$, $p=n.s.$) estimated using all channel data. The pattern was the same when we examined the peak alpha frequency using only the frontal channels or only the posterior channels (all $r<.16$, $p>.34$); see Figure 2C .

Based on the IAF method, the average range for the lower alpha frequency1 (low alpha1; defined as $pA-4$ to $pA-2$) was 5.54 to 7.53Hz, lower alpha 2(defined as $pA-2$ to pA) was on average 7.53 to 9.54Hz; and high alpha (defined as pA to $pA+2$) was on average 9.54 to 11.53Hz. The average baselined alpha power using the IAF method are shown in Figure 6. As can be seen in the figure, the low alpha 1 shows a drastically different pattern of activity than the low alpha 2 and high alpha frequency bands (more formal comparisons are done below).

Change Detection Data

Average power for the CD task is shown in Figure 7A. First we ran a repeated measures ANOVA with time (6 time-bins), condition (set-size), and frequency (3 frequency bands) as within-subject factors. We found a significant main effect of time ($F(2.59,85.51)=49.11$, $p<.01$), and frequency ($F(2,66)=35.91$, $p<.01$), but not condition ($F(3,99)=0.09$, $p>.05$). When we constrained our analysis to just the

retention-period activity, we found a small but significant main effect of condition ($F(3,99)=2.87, p<.05$). All interaction terms were also significant (all $p<.01$). There was no significant effect of baseline activity between conditions ($F(3,99)=2.36, p=.08$). Paired t-tests showed that the lowest alpha frequency, mean alpha level1 (pA-4 to pA-2), differed from both low alpha level2 (pA-2 to pA) and high alpha (pA to pA+2) ($t(33)>6.72, p<.01$); however low alpha level2 did not differ from high alpha ($t(33)=0.70, p>.05$).

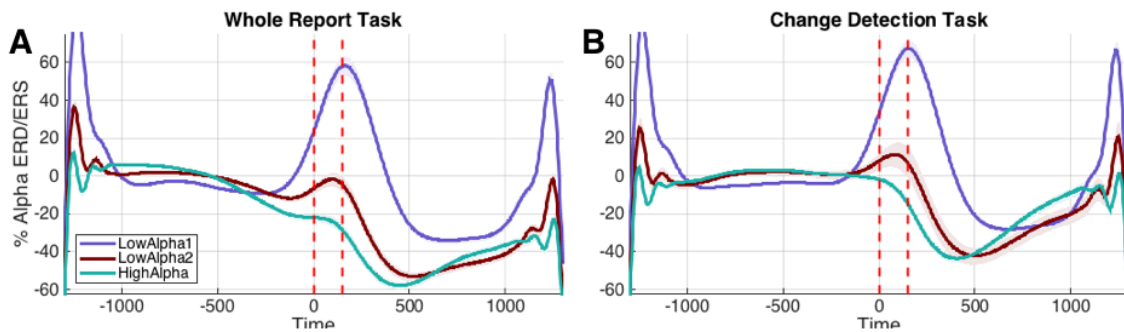


Figure 6: Alpha percentage ERD/ERS split by individualized alpha frequency bands. Low Alpha1 represents a band 4Hz to 2Hz below each individual's peak alpha frequency (pA-4 to pA-2). Low Alpha2 represents 2Hz to peak frequency (pA-2 to pA). High Alpha represents the peak frequency to 2Hz above band (pA to pA+2)

Examining the average alpha ERD/ERS (collapsing over all three individualized frequency bands and set-sizes) we found a significant decrease in power (ERD) compared to baseline from 356ms to the end of the trial (all $t(33)>4.58, p<.01$), and a significant increase in power (ERS) in the -116ms to 120ms time bin (the time bin corresponding to the display of the memory array). When we split the data by set-size, set-size 1 remained significant in the 356 to

828ms time period ($t(33)=6.04, p<.01$); while set-sizes 2-6 ERDs remained significant from the 356ms to the end of the trial (all $t(33)>3.67, p<.01$).

When we separated the data into the three alpha-frequency bands we found that all three frequency bands exhibited a significant level of ERD during the retention interval (alpha level1: set-sizes 1, 3, and 6 were significant from 592 to end of trial, set-size 2 was significant from 592ms to 828ms (all $t(33)>5.69, p<.01$); alpha level2: set-size 1 was significant from 356ms to 828ms, set-sizes 2-6 were significant from 356ms to the end of the trial (all $t(33)>3.55, p<.01$); high alpha: set-sizes 1-3 were significant from 120ms to 828ms, set-size 6 was significant from 120ms to the end of the trial (all $t(33)>3.69, p<.01$). As is evident in Figure 6A, the lowest alpha frequency (low alpha1) also exhibited a significant synchronization (ERS) in the -116ms to 356ms time interval ($t(33)>4.66, p<.01$).

Comparing between the ERD/ERS profiles of each frequency band, we found a significant difference between the low alpha1 band and the low alpha2 bands; between these two bands the significant difference in ERD/ERS for all set-size conditions occurred in the -116ms to 592ms time period ($t(33)>4.13, p<.01$). When comparing the low alpha2 and the high alpha band, we only found significant differences in the ERD levels during the 120ms to 356ms time periods for set-sizes 2-6 ($t(33)>3.75, p<.01$). It is important to note that these differences only represent percentage differences from the baseline power, and are not necessarily indicative of no differences in overall power between the frequency bands.

We found a significant difference in ERD values between CD accurate and

inaccurate trials. Across all set-sizes and frequency bands, alpha ERD was lower (greater desynchronization) for accurate relative to inaccurate trials from -116ms to the end of the trial ($t(33) > 3.12$, $p < .01$). If we separate the data by condition (set-size), only set-size 3 trials showed a significant difference between accurate and inaccurate trials ($t(33) > 3.63$, $p < .01$; from -116ms to 592ms); though set-size 2 also showed a substantial difference from -116ms to 828ms ($t(33) > 2.62$, $p < .02$ *).

Whole-Report Data

Average alpha power for the whole-report task is shown in Figure 7B. A repeated measures ANOVA revealed significant main effects of condition ($F(2.46, 45.30) = 3.51$, $p < .03$), frequency ($F(1.37, 45.30) = 52.24$, $p < 0.01$), and time ($F(2.35, 77.65) = 59.54$, $p < .01$). All interaction terms were also significant (all $p > .001$). Pairwise comparisons of frequency showed a significant difference between all three of the frequency bands ($t(33) > 2.98$, $p < 0.05$); conditions (set-size) showed a significant difference only between set-size 2 and set-size 3 ($t(33) = 3.40$, $p < .02$), and a trending difference between set-size 1 and set-size 3 ($t(33) = 3.14$, $p = .06$).

Time bin comparisons showed a significant ERD from 356 to the end of the trial (collapsing across power bands and set-size conditions; $t(33) > 8.47$, $p < .01$). Surprisingly, we did not find any evidence of an ERS response for the time bin corresponding to the memory display ($t(33) = 0.33$, $p > .05$). When we split the data into set-size conditions we found the exact same pattern; for all set-sizes the power was significantly reduced from 356ms to the end of the trial ($t(33) > 5.25$, $p < .01$).

Separating the three individualized alpha frequency bands, we found that the

lowest frequency (low alpha1) was significantly reduced from baseline from the 592 to the end of the trial (all set-sizes: $t(33) > 4.40$, $p < .01$); furthermore, this frequency band showed a significant increase in power (ERS) for all set-sizes in the -116ms to 356ms trial period (all $t(33) > 3.27$, $p < .01$). The middle alpha band (low alpha2) and higher alpha band showed very similar patterns of activity; there was a significant reduction in power from 356ms to the end of the trial for the low alpha2 frequency (all $t(33) > 4.83$, $p < .01$) and from 120ms to the end of the trial for the high alpha frequency (all $t(33) > 3.84$, $p < .01$).

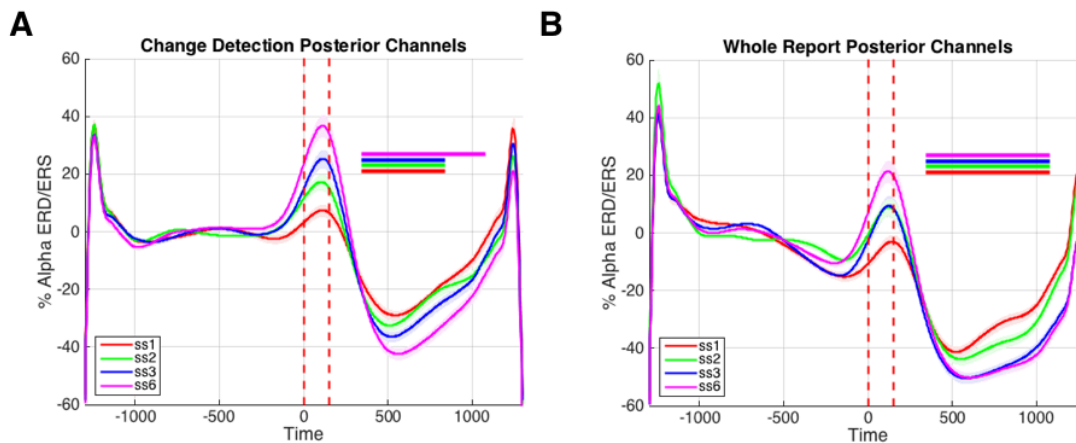


Figure 7: Average of the three alpha frequencies estimated using the IAF method. A) Change detection ERD/ERS percentage. B) Whole report ERD/ERS percentage estimates from baseline. Shading represents the standard error of the mean; colored horizontal bars represent significance from baseline.

We found a significant difference between the low alpha1 band and the low alpha2 band in the -116 to 356ms time period (all $t(33) > 3.68$, $p < .01$). When comparing low alpha2 and high alpha2, we found a significant ERD difference in the -116ms to 356ms time bin only during set-size 3 and set-size 6 trials (all $t(33) > 4.54$, $p < .01$).

Examining accuracy, we found a significant difference in alpha ERD between low accuracy (partial lapse: 0,1 or 2 correct) and good trials (3 or more correct) from 592ms to the end of the trial (all $t(33) > 3.23$, $p < .01$).

Discussion

The current study used a change detection and whole-report task to assess how alpha-frequency oscillations are modulated when participants are performing a typical VWM task. Results of two analyses show that alpha power decreases as information is retained in working memory. Interestingly, the results show a strikingly similar pattern regardless of whether we used unbaselined alpha power or an individualized alpha frequency analysis (IAF). Furthermore, it was shown that alpha power is increasingly reduced (desynchronized) with increasing number of items in the memory array, and we saw hints of greater desynchronization during accurate representations of the memory displays. Together, these findings suggest that alpha desynchronization can serve as an index of working memory processing while participants are performing a VWM task.

In our first iteration of the analysis, we concentrated on unbaselined alpha power calculated over the typical 8-12Hz range. Using this method, we saw a significant reduction in alpha power starting at 120ms of stimulus onset. This reduction was set-size and accuracy dependent, such that higher set-sizes and higher accuracy in the whole-report task showed greater levels of alpha suppression. Importantly, this trend was similar in both the CD and whole-report tasks: the individuals who exhibited the strongest modulation of alpha in the CD task also exhibited a strong modulation of alpha in the whole-report task. This

result, along with a strong relationship between CD and whole-report behavioral performance, corroborates and extends our previous work showing that CD and whole-report measure the same cognitive construct (Adam et al., 2015).

Inconsistently with previous findings, we found no evidence that peak alpha frequency is related to behavior accuracy in either the CD or the whole-report task. There are a number of reasons for why this could occur. First, our IAF estimate was derived from the baseline periods preceding each trial, instead of a typical eyes-closed rest period. It could be that our baseline method is a non-optimal way for estimating each individual's peak alpha frequency. Secondly, our sample may have been too homogenous. Peak alpha frequency has been reported to vary between different age groups, special populations, and individuals with different levels of cognitive ability (Klimesch, 1999). Our sample was composed primarily of college students, all between 18-35 years of age; thus, it could be that our sample was not diverse enough for us to detect a reliable relationship between peak alpha power and VWM ability. Thirdly, the correlation between peak alpha frequency and behavior may be task-specific. To our knowledge, most studies using an IAF analysis based on peak alpha frequency have tended to find a significant correlation with performance on tasks using verbal or alpha-numeric memory arrays (Klimesch, et al., 1997; 1999). Even though some of these experiments have aimed to minimize semantic encoding (Klimesch et al., 1999), the verbal nature of the stimuli may have still promoted some phonological encoding. Consequently, this leaves a small possibility that the relationship between peak alpha frequency and cognitive performance may not be detectable when participants are performing a primarily

visual working memory task.

Despite the lack of correlation between peak alpha and behavior, we observed similar significant changes in the profile of the alpha ERD/ERS as we did using unbaselined alpha power. This result somewhat conflicts with work showing greater synchronization of alpha power with memory load. Again, the reasons for why our results differ from those previously reported in the literature may come down to the nature of our tasks. First, we should bear in mind that the duration of our stimulus displays (150ms) is much shorter than many other tasks used to examine alpha power and working memory (for example 3000ms in Klimesch et al., 1999). Furthermore, our retention duration (1150ms) is also much shorter than previous studies (for example, 6000ms). Taking into consideration both a shorter presentation duration and retention period, our task may have led to differences in the working memory processes that people recruit to perform the task. Furthermore, as mentioned previously, the stimuli in the current study are very different from random number/letter sequences and word lists used in previous studies (Bastiaansen, et al., 2001; Bonnefond & Jensen, 2012). The impact of task stimuli may be considerably important when examining alpha power, which is particularly sensitive to visual processing (Bollimunta et al., 2008, 2010).

Even though the current results do not show greater synchronization with greater working memory load, they do corroborate the more general finding that the modulation of alpha power tracks the contents of working memory (Hanslmayr & Staudigl, 2014; Jensen et al., 2002; Klimesch et al., 1997; Klimesch, Schimke, & Schwaiger, 1994; Pava et al., 2011). The current results extend this research by

showing that desynchronization of alpha power over the occipital cortex indexes the number and successful recall of items in VWM using a task that is routinely used to estimate working memory capacity.

Given the current task, there are several reasons for why alpha desynchronization, instead of synchronization, is a more likely index of the content of VWM. First, there was no explicit distracting information in our task. All items presented in the memory-array had an equal probability of being probed in the CD task, and all items had to be recalled in the whole-report task. Accordingly, though alpha may serve as a gating mechanism for suppressing irrelevant visual information from being processed (as evidenced by synchronization), this mechanism was not particularly necessary in the current task. Second, it has been well documented that alpha oscillations are especially prominent over the occipital cortex. Indeed, recent studies suggest that circuits in the occipital cortex and thalamus are optimally organized to engender alpha frequency oscillations (Mo, Schroeder, & Ding, 2011). In addition, a growing number of investigations have shown that visual areas that are responsible for the encoding of visual information are also involved in working memory maintenance (Ester, Serences, & Awh, 2009). Thus, a parsimonious account of our findings is that the observed decrease in power represents the perturbation of neurons in the visual cortex that code for visual features in the memory array. As described in the introduction, this desynchronization of cortical neurons may be a necessary mechanism for the ability to represent multiple items in memory (Axmacher et al., 2010). Therefore, the desynchronization of neurons in the visual cortex, which innately display high

degree alpha synchronization (Spaak et al., 2012; Suffczynski, et al., 2001), is a critical feature of being able to represent items in working memory.

Though we saw a few hints that alpha power, particularly towards the end of the trial, is related to behavioral performance, the results were somewhat inconsistent. For example we saw significant differences between low accuracy and high accuracy trials in the whole-report task using unbaselined alpha power and using the IAF method. However, using the unbaselined data, we did not observe consistent differences between accurate and inaccurate trials in the CD task. However, it is important to note that change detection does not provide a fine assessment of how many items individuals were representing during a particular trial. That is, during any particular trial there are several reasons why an individual fails to detect a change, or inappropriately detects one. One is that the individual did not remember any of the items in the memory array (indicative of an attention failure). Another possible reason is that the individual remembered a fair number of items, but was probed on an item that they did not remember. The CD task does not distinguish between these two possibilities. Consequently, a fair number of the incorrect trials examined could still be trials in which the individual remembers a good amount of information, which make it difficult to distinguish between good versus bad trials using alpha power. There is some evidence that this could be the case in our data. When we examined the accuracy differences by set-size, we saw that we could distinguish between accurate and inaccurate trials in the set-size 2 and 3 conditions (using the IAF method), but not in the set-size 6 condition. One plausible explanation for this finding is that during a set-size 2 or 3 trial, an

incorrect response in the CD task is likely to reflect a failure of attention since in these trials the memory arrays are at or below capacity. However, during a set-size 6 trial, an incorrect response could either reflect an attention failure or an unlucky probe target.

The whole-report task circumvents the ambiguity present in the CD task by directly testing how many items are being represented on a trial by trial basis. Using this task, we found consistent differences between good and bad trials towards the end of the retention period. This finding was somewhat weaker in the unbaselined data, but this may have simply been because our analysis bins were far too coarsely graded. Recent findings from our lab have shown that differences between good versus bad trials in unbaselined data typically emerge in the last hundred milliseconds of the trial. Thus, our pooling of alpha activity into 236ms time bins may have weakened the observed effect.

Conclusions

The goal our first experiment was twofold. First, we wanted to examine how alpha oscillations vary within a change detection and whole-report task, two tasks that provide reliable measures of working memory capacity. Secondly, we wanted to be able to compare our results with those in the recent literature. In regards to our first aim, we found that alpha power desynchronizes when individuals represent items in working memory. Furthermore, this desynchronization is set-size and accuracy dependent, such more information in memory results in greater reductions of alpha power, and accurate trials exhibit larger decreases of alpha

power. To be able to compare our results with relevant findings in the literature, we ran an IAF analysis based on the individual dominant frequency of each participant (Klimesch et al., 1997). This analysis produced very similar findings to the results based on unbaselined alpha power data.

Overall, the current data suggest that alpha power decreases are related to the representation of items in working memory. Surprisingly, one of the first studies to observe this negative relationship between alpha power decreases and memory performance was conducted by Klimesch (Klimesch et al., 1996). In this study, Klimesch and colleagues used the IAF method to demonstrate that decreases in lower alpha power during encoding are positively related to subsequent recall to the memory items. This finding has been well corroborated by other studies in the long term memory literature (Hanslmayr, Staudigl, Fellner, 2012). The current study extend this research by showing that alpha-power decreases are not exclusively related to semantic encoding (for example, see Hanslmayr et al., 2009), but are also related to performance in a VWM task.

The desynchronization of alpha makes intuitive sense in regards to how working memory items are individuated. Given the prominent theory that synchronized activity between neural populations reflects the binding representations into one distinct unit, the desynchronization of firing is an effective way of avoiding unwanted crosstalk between distinct neural assemblies (Klimesch, Sauseng, & Hanslmayr, 2007). Some support for this idea has been shown in studies using intracranial EEG recordings. For example, Sederberg and colleagues (Sederberg et al., 2007) have demonstrated that the accurate retrieval of words in a delayed

free recall task was associated with decreased alpha power in the hippocampus and the left inferior prefrontal cortex, two areas associated with working memory processing (Axmacher et al., 2010; Braver et al., 2007; Fell et al, 2001; vanVugt et al., 2010).

The current findings also indicate that the IAF method may be an unnecessarily complicated method of estimating alpha modulation in a VWM task. To begin with, we should consider that we did not find any reliable relationships between peak alpha frequency and behavioral performance. This suggests that using the peak alpha frequency as an individualized anchor of distinct alpha bands may not be necessary, especially in tasks similar to ours. Furthermore, the two upper alpha frequency bands (low alpha2 and high alpha) did not show remarkably different profiles in either one of our tasks. The common argument for why alpha power should be parsed into distinct frequency bands is that the lower and higher alpha bands show distinctly dissimilar profiles, with lower alpha indexing attentional processing, and higher frequency alpha indexing semantic processing (Klimesch et al., 1997; Klimesch, Schimke, & Schwaiger, 1994). It could be that the visual nature of our task changes the encoding processes that these distinct alpha bands reflect, thereby making it unnecessary to distinguish between the two frequencies. Lastly, we should note that the lowest of the alpha frequencies (low-alpha 1) showed a very different profile from the two higher frequencies. In fact, the estimated frequency band of this lower alpha is much more aligned with what is typically considered theta power, and also shows power fluctuations that more closely resemble theta (Adam et al., 2015). As a result, an argument could be made

that pooling this low alpha frequency with the two other bands distorts the overall alpha signals in the current tasks. Given that the IAF ERD/ERS method did not produce drastically different results from our unbaselined data, the rest of our analyses will concentrate on the unnormalized, typically-defined alpha frequency of 8-12Hz.

One critical feature of our design that may restrict our ability to compare the current findings with those in the literature is that all items in the memory displays were relevant. As mentioned previously, alpha oscillations have been shown to be critical to the suppression of irrelevant information. This makes it difficult to conclude whether we would ever see a synchronization signal (indicative of suppression) in a working memory task. This question will be addressed in the following chapters.

CHAPTER III: THE ROLE OF DISTRACTERS

Introduction

The previous experiment indicated that the desynchronization of alpha-frequency oscillations is related to representation of information in working memory. However, a prominent theory in the literature is that alpha oscillations reflect an active suppression of irrelevant information. This theory has been supported by multiple studies showcasing that an increase in alpha-power (synchronization) is associated with better suppression of distracting information in visual (Min & Herrmann; 2007), auditory (Banerjee, et al., 2011; Krause et al., 1996), and even long-term memory tasks (Waldhauser, Bäumi, & Hanslmayr, 2014). Furthermore, greater pre-stimulus alpha power is associated with unawareness of task-relevant targets (Händel, Haarmeier, & Jensen, 2011), indicating that alpha power is functionally related to the perception of incoming information (Bauer et al, 2014; Song et al., 2014; vanDijk et al., 2008; VanRullen & Macdonald, 2012).

Given this predominant view of alpha power, a necessary test of the function of alpha oscillations in VWM is to examine how they are modulated by irrelevant information. This will be the topic of the following two experiments.

Experiment 2A: Remember-N Experiment

In this study, we test how alpha frequency oscillations track the number of relevant VWM representations while irrelevant items are also present on the screen. One potential criticism of our first experiment is that alpha may only track the

number of items on the screen, instead of the number of relevant VWM representations. That is, the number of items on the screen was confounded with the number of items that individuals had to remember; this makes it difficult to distinguish whether the alpha signal is related to just the perception of items or whether it is related to the number of internal representations. To examine this question, the current experiment used a cued memory design, which we will call 'Remember N' task. In this task, participants were presented with six items on the screen, and on every trial they were instructed on how many of the items (out of six) they should remember.

The design of this experiment allowed us to test two critical features of alpha. First, it allowed us to examine whether alpha is modulated by number of items on the screen, or the number of items in memory. Second, it allows us to test the inhibition theory of alpha oscillations. With the current design, one could consider all items that are not to be remembered as distractors. For example, when participants are cued to only remember one item, five items on the screen are essentially distractors. If the primary role of alpha oscillations is to suppress irrelevant information from being encoded, we should find considerable evidence for suppression (as indicated by alpha synchronization) in the current design. Furthermore, this suppression effect should be set-size dependent, such that we see a greatest amount of suppression for set-size 1 trials, in which five items are irrelevant versus set-size 2 trials, where only four items are irrelevant, and we should observe the least amount of suppression during set-size 6 trials, when all items are relevant.

Methods

Methods were similar to the first experiment, with the following exceptions.

Participants:

31 new participants (18-35 years old) took part in this study; 7 participants were excluded from the analysis due to an excessive number of artifact-rejected trials. The final sample comprised of 24 participants.

Experimental Task:

The experimental task was similar to the whole-report task run in the first experiment (see Figure 8). The primary difference was that preceding the start of each trial, participants were given a cue indicating how many of the items in the memory array to remember and later recall. They were instructed to try their best to only remember the number of cued items and ignore the rest. Participants were not instructed on which item (of the six presented on every trial) to remember; the selection was always left up to the participant. During the response, participants only had the option to respond to as many items as they were cued to remember (for example, if the cue was “remember 1”, they could only make one response during the recall phase). The cue for the next trial was given 1000ms after the participant had made all responses. Participants self-initiated the next trial by pressing the spacebar. Participants performed a total of 150 trials per set-size (set-sizes 1, 2, 3, and 6), for a total of 600 trials over 20 experimental blocks.

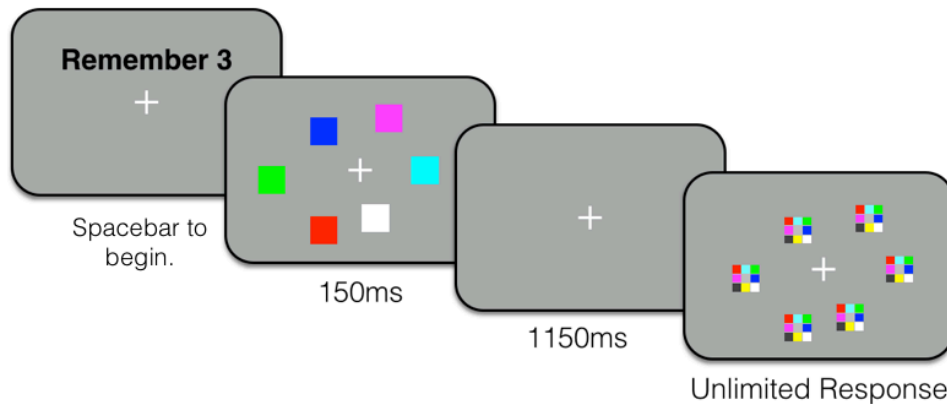


Figure 8: Experiment 2A: “Remember N” task procedures. At the beginning of every trial participants were given a cue as to how many items to remember from the upcoming memory array. Memory arrays always contained six items shown in random locations; at response participants only recalled as many items as they were asked to remember.

Estimation of EEG Power

Data was analyzed using a Hilbert transform, outlined in the first experiment.

This analysis is especially appropriate for the current experiment because the baseline period (preceding the memory array) may differ between conditions due to the ‘remember n’ cue given at the beginning of the trial. Statistical relevance was again assessed by averaging the trial data into 236ms time bins.

Results

Behavioral Results

Mean capacity (K) in this task was 2.75 (SD=0.40).

EEG Results

The average alpha power is shown in Figure 9A. A repeated measures ANOVA with time (4 retention interval time bins) and condition (4 set-sizes) indicated a significant main effect of time ($F(1.56,35.86)=7.26, p<.01$), condition

($F(2.0,10.17)=4.42, p<.02$), and significant interaction ($F(1.78,40.94)=5.84, p<.01$). Importantly, when we examined just the baseline power or stimulus display period, we did not find any significant differences between conditions ($F(2.16, 50.23)=1.35, p>0.05$, and $F(1.78,41.34)=1.01, p>.05$ respectfully).

Paired comparisons on the overall alpha fluctuation revealed a significant difference from baseline from 120ms to 828ms (all $t(23)>3.35, p<.01$). Comparisons within each condition revealed a significant desynchronization from 120ms to 592ms in the set-size 1 condition ($t(23)>3.28, p<.01$); from 120ms to 828ms in the set-size 2 condition ($t(23)>3.25, p<.01$); 120ms to the end of the trial for the set-size 3 condition ($t(23)>3.27, p<.01$), and 120ms to 828 for the set-size 6 condition, though this last time window just shy our adjusted significance threshold ($t(23)=3.18, p<0.01^*$).

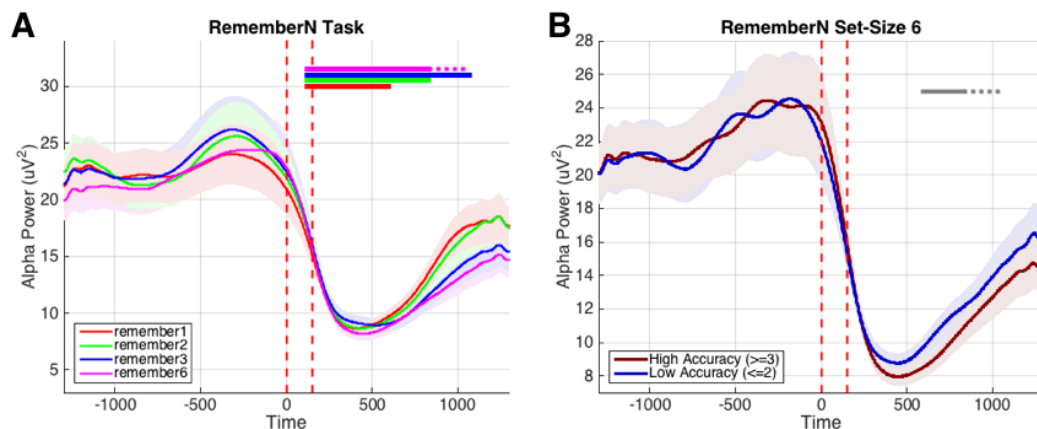


Figure 9: Experiments 2A results: A) Alpha power across set-sizes; horizontal colored bars represent significance from baseline. B) Low accuracy vs. good accuracy trials in the ‘remember-6” condition; horizontal grey lines represent time-bins showing a significant difference between low and good accuracy. Dotted lines represent a marginally significant effect.

Comparing between conditions we found a significant difference between set-sizes 1 and set-size 6 trials ($t(23)=3.10$, $p<.05$), and the set-size 2 and set-size 6 trials ($t(23)=3.01$, $p<.05$). No other comparison were significant (all $t(23)<1.45$, $p>0.35$)

To examine accuracy, we restricted our analysis to set-size 3 and set-size 6 trials, and estimated whether we could detect a significant difference between low accuracy trials (accuracy less than or equal to 2 items) and good trials (accuracy above or equal to 3 items) . We found that we could distinguish between bad and good trials in the set-size 6 condition ($F(1,23)=5.84$, $p<.05$), but not in the set-size 3 condition ($F(1,23)=0.12$, $p>.05$). For set-size 6, the difference between good and bad trials emerged primarily towards the end of the trial (592ms to 828ms time period, $t(23)>2.88$, $p<.01$), see Figure 9B. When we combined data for both conditions, we could no longer distinguish between good and bad trials between them, though the effect was trending ($F(1,23)=3.77$, $p=0.06$). The difference between set-size 3 and set-size 6 trial accuracy was confirmed by a significant interaction between accuracy and set-size in a repeated measures ANOVA with accuracy (good/bad trial signal), set-size (3 versus 6), and time (last 2 time bins: 592ms to 1064ms) as factors ($F(1,23)=4.71$, $p<.05$). This discrepancy in our ability to distinguish between good or bad trials between the two set-sizes cannot be attributed to differences in the number of trials; for both set-sizes, approximately a third of trials were lapses (mean lapse rate set-size 3: 34.81%; mean lapse rate set-size 6: 32.67%; $t(23)=1.82$, $p=.08$).

Discussion

This experiment allowed us to examine two different features alpha oscillations. First, it allowed us to examine whether alpha tracks the number of items on the screen, or the number of items retained in memory. To examine this, we held the number of items that individuals saw constant, while manipulating the number of items that individuals were to retain in memory. We found that alpha frequency oscillations are primarily influenced by the number of items in memory, as evidenced by a significant difference between conditions. If alpha power was primarily reflecting the number of items on the screen, we should have found no differences between any of our ‘remember n’ conditions.

Additionally, the current paradigm allowed us to examine whether irrelevant information leads to alpha synchronization, as the inhibition hypothesis would predict. We found no evidence of an increase in alpha power for any of the set-size conditions. Instead, in all conditions we found a significant decrease in alpha power during the memory retention period. Of course, it still could be argued that synchronization did have a role in our task, even leading to the power differences between conditions that we observed. For example, a one could argue that the low amount of power reduction for set-size one versus higher set-sizes could be driven by higher synchronization during set-size one trials, since during these trials, there are more irrelevant items on the screen than there are for higher set-sizes. However this argument would have to rest on the assumption that the magnitude of desynchronization at low set-sizes still overpowers the synchronization signals, leading to a net reduction in power. It is difficult to distinguish between the specific

quantity of synchronization versus desynchronization in the current experiment, and given the ubiquity of neural circuits that exhibit alpha (Meltzer et al., 2008), both types of modulation are probably occurring. All we can conclude from the current results is that the power of alpha-frequency oscillations decreases during working memory processing, and it does so in a load-dependent instead of stimulus-dependent manner.

A possible criticism of the current experiment is that during every trial, all stimuli presented could be possible targets (the subjects could choose any of the items to remember). Consequently, none of the items are true ‘distractors’, and this could lead to a reduction in the inhibition function of alpha. In our next experiment, we directly test this possibility.

Experiment 2B: Filtering Experiment

In the current experiment, we directly test the theory that alpha frequency oscillations serve to suppress extraneous items from being encoded into working memory. We test this hypothesis by having individuals perform a working memory task, while filtering irrelevant items from being represented. If the role of alpha is primarily to suppress information, then we should find evidence of a synchronization signal during distractor-present versus no-distractor trials. Conversely, if alpha frequency oscillations reflect the encoding of relevant items, distractors should have little influence on the observed signal.

Methods

All methods are similar to Experiment 2A, with the following exceptions:

Participants

26 new participants partook in the study; 2 participants were excluded from the analysis due to an excessive number of artifact-rejected trials. This left 24 participants in final sample.

Experimental Task

The experimental paradigm is shown in Figure 10. Participants were asked to remember the orientation of a gap on colored circular stimuli. The orientation of the gap for each stimulus was always in one of the cardinal directions (up, down, left, right); repetitions of orientations within a trial were allowed. Half of the participants were directed to attend to only the blue items, and half were asked to attend to only the green items. On half the trials, the target stimuli (blue or green items) were presented without any distractors; on the other half of the trials, items with the opposite color were presented as distractors. Participants responded by clicking on lines corresponding to the orientation of the gap on the memory-set stimuli. They were presented with either 1, 2, 3, or 4 target items; when distractors were present, they were equal to the number of targets during that trial (for example on a set-size 2 trial, there would be two target and 2 distractor items). Distractor-present and distractor-absent trials were always randomized within blocks. Participants performed a total of 640 trials over 20 blocks; there were 80 trials per set-size without distractors, and 80 trials per set-size with distractors.

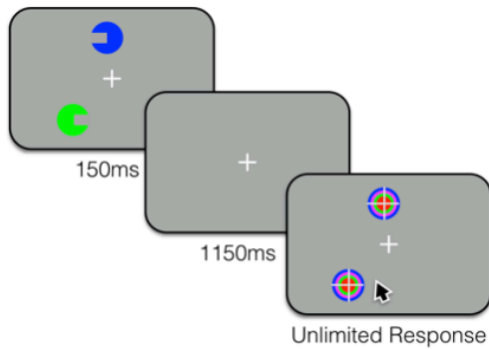


Figure 10: Experiment 2B: Filter experiment task procedures. Shown is an example of a distractor present trial. Participants were told to remember the location of the gap for either blue or green items, and ignore the irrelevant color. Following the brief retention period, participants used the mouse to click on the bar that corresponded to the location of the gap on the relevant items.

Estimation of EEG Power

Similar to Experiment 2A, instantaneous alpha power was estimated using a Hilbert transform (see Experiment 1 for details).

Results

Behavioral Results

Capacity (using set-size 3 and 4 trials) for distractor-absent trials was 3.22 (SD=0.17), capacity for distractor-present trials was 3.09 (SD=0.22). There was a significant correlation between these two capacity measures ($r=0.96$, $p<.01$, 95%CI: [0.91, 0.98]). The difference between them was also significant ($t(23)=8.36$, $p<.01$).

EEG Results

Average power for the distractor absent and present is shown in Figure 11A and 11B. A repeated measures ANOVA with distractor (present/absent), set-size, and time (four 236ms time bins corresponding to retention-period activity) as factors showed marginally significant effect of distractor-condition ($F(1,23)=4.39$, $p=.05$),

and significant main effects of set-size ($F(1.57,36.18)=10.10, p<.01$), and time ($F(1.66, 38.26)=4.92, p<.02$). The interaction between distractor-condition and set-size was not significant ($F(1.48,34.18)=.78, p>.05$), and the interaction between distractor-condition and time was marginally significant ($F(1.45,33.26)=3.49, p=.06$). The interaction between set-size and time was significant ($F(2.93, 67.50)=4.24, p<.01$). Baseline power values did not vary between either distractor conditions or set-sizes (all $t(23)<2.15, p>.05$).

Collapsing across all conditions, we found a significant reduction in power from 120ms to 828ms (all $t(23)=3.03, p<.01$). This effect remained the same when we split the data into distractor-absent (all $t(23)>3.01, p<.01$) and distractor-present trials (all $t(23)>3.07, p<.01$). If we split the data into separate conditions, none of our comparisons survived our adjusted alpha threshold ($p<.0016$). For this reason, the rest of our analysis uses a less conservative threshold ($p<.01$). In the distractor-absent condition, all set-sizes exhibited a significant reduction in alpha power from 120ms to 828ms (all $t(23)>2.87, p<.01$); set-sizes 1 and 4 were also significant during the 828ms to 1064ms interval (all $t(23)>2.86, p<.01$). In the distractor-present condition, all set-sizes exhibited a significant reduction in power from 120ms to 592ms; with set-sizes 3 and 4 remaining significant until the end of the trial (all $t(33)>3.02, p<.01$).

Next, we compared between distractor conditions at each set-size. We found a significant difference between set-size 1 and set-size 2 distractor-absent and distractor-present conditions in the 356ms to 592ms time period ($t(23)=2.61, p<.02$). There was no significant difference between the set-size 3 distractor-

absent/present trials ($t(23) < 1.65$, $p > .05$); while set-size 6 showed a significant difference in the 356ms to 828ms time period ($t(23) > 2.60$, $p < .02$).

Comparing the set-size 2 distractor-absent condition with the set-size 1 distractor-present condition (both consisted of presenting 2 items on the screen), we found no difference between the two conditions during any time bin ($t(23) < 1.01$, $p > .05$), see Figure 11C. Comparing the set-size 4 distractor-absent condition with the set-size 2 distractor-present condition (both having 4 items on the screen), we found a significant difference from 592ms to the end of the trial ($t(23) > 2.65$, $p < .01$), see Figure 11D.

Next we examined whether accuracy affected the amount of alpha desynchronization observed. We found no significant difference between good or bad trials in any condition (set-sizes 3 and 4 in both distractor conditions) (all $t(33) < 2.0$, $p > .05$). It is important to note that since we only tested set-sizes 1-4, accuracy in the current experiment was fairly high, and participants had a much lower percentage of low-accuracy trials than observed in the previous experiment (16% of trials in the distractor-present condition, and 10% of trials in the distractor-absent condition).

Lastly, we examined whether performance in the task was related to the amount of desynchronization difference between distractor-absent and distractor-present trials. To do so, we collapsed across set-size conditions and examined whether higher- and lower- performing subjects (based on a median split analysis of performance in the distractor-free trials) exhibited a difference in the desynchronization profiles. We found hints that low-performing subjects had

greater alpha desynchronization during the distractor-present condition in the 356ms to 592ms time bin ($t(11)=2.76, p<.02$). However, this result should be interpreted with caution; first, the median split analysis greatly decreased our sample sizes, and secondly, the median split was based on performance within the filtering task itself. Additional experiments with a greater number of subjects and a separate working memory task are necessary to examine if this effect persists.

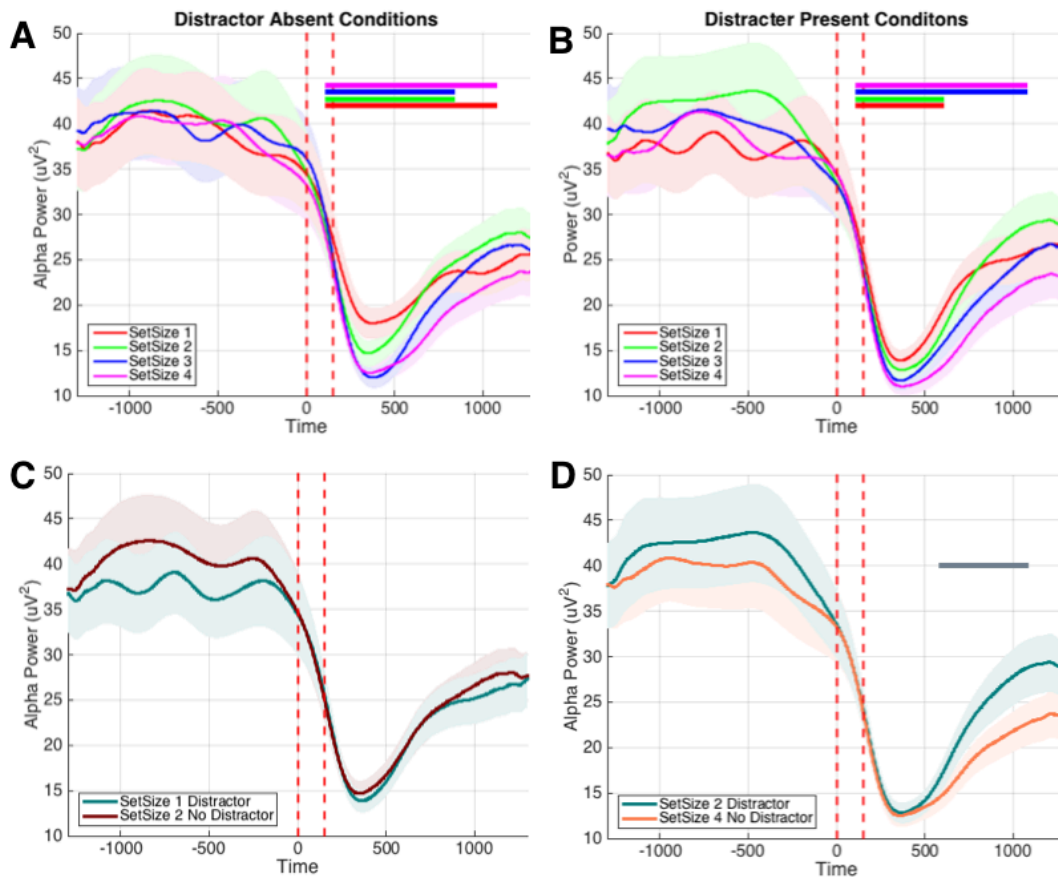


Figure 11: Experiment 2B alpha desynchronization by set-size for A) distractor absent and B) distractor present trials. Horizontal lines represent significant reduction from baseline. Equating for the number of items on the screen we observed different results for lower vs. higher set-sizes: C) set-size 1 distractor present and set-size 2 distractor absent trials, D) set-size 2 distractor present and set-size 4 distractor absent trials.

Discussion

The current experiment specifically tested whether alpha-frequency oscillations exhibit a synchronization of activity during a working memory task that requires filtering. We found no evidence of greater synchrony when distracter items were present. In fact, we found that the distractor-present conditions exhibit a slightly greater reduction in alpha power in the earlier stages of the retention period. This finding may indicate that on some trials, participants were less efficient at filtering, and possibly encoded some of the irrelevant items. This slightly greater desynchronization may also reflect another cognitive process related to filtering or updating the current memory set (Manza et al. 2014). Irrespective of the process that this desynchronization reflects, we found no evidence that the need to suppress distractors leads to greater synchronization of alpha-frequency oscillations.

An interesting finding in the current results is that set-size 1 distractor-present and set-size 2 distractor-present trials did not significantly differ across any time bin. While set-size 2 distractor-present and set-size 4 distractor-absent trials substantially differed towards the end of the trials. In both instances, participants were viewing an equal number of items (two in the first and four in the second), while the number of relevant target items differed. The difference in the alpha power pattern between these set-sizes seems to suggest that at very low set sizes (for example set-size 1), participants may still encode the irrelevant items, while at higher set-sizes, they begin to filter irrelevant distractors. This may help explain why we did not find a significant difference between 'remember 1' and 'remember 2' trials in Experiment 2A; here, given the relatively low demand of remembering only

one item, participants may have encoded more items.

Based on the current results, we propose that the function of alpha depends on the demands of the task. In a VWM task, when incoming visual information is inherently important to the task at hand, desynchronization of alpha is related to the processing of task-relevant visual items. When visual information is not as important and may interfere with the maintenance of information already in memory (Jensen et al., 2002), alpha synchronization may reflect the active gating of additional visual information from entering memory (Klimesch, et al. 2007).

Conclusions

In two different visual working memory tasks, we demonstrate that alpha-band activity over occipital regions is modulated by the number of relevant items in memory. Importantly, we found no evidence that the alpha signal is influenced by the number of irrelevant items on the screen. The insignificant impact of extraneous items was found in both our first experiment, where all items could be potential targets, and in the second experiment, which contained specific distractor items. These findings strongly indicate that in a visual task, alpha frequency oscillations are related to the information currently represented in memory, rather than the suppression of irrelevant distractors.

In the context of what has been previously observed by other experiments, our results replicate previous findings showing an overall decrease of alpha power relative to baseline (Hanslmayr et al., 2005; Palva et al., 2011). However, they conflict with results showing a general increase in alpha power with set-size (Jensen et al., 2002).

Our cue and distractor manipulations allowed us to examine the influence of working memory processing in the face of irrelevant information, as a means of testing the dominant hypothesis that that alpha power increases are a requisite for suppressing task-irrelevant memories from being formed (Gray et al., 2015; Klimesch et al., 2007; Womelsdorf & Fries, 2007). We hypothesized that if increases in power reflect distractor suppression, we should find that the presence of irrelevant information should lead to greater levels of alpha power, and that this effect should be set-size dependent. In our first experiment, we saw that higher set-sizes exhibit higher levels of alpha desynchronization. Critically, even the lowest set-sizes, in which there were substantially more potential distractors versus targets exhibited a significant reduction in power from baseline. It is also important to note that in this task participants were aware of the total number of items in the display (always 6) and how many items they should remember. This shows that even in the lower set-sizes, when individuals knew before initiation of the trial that they had to suppress a substantial number of the to-be-displayed items, we still observed a reduction in alpha power.

A recent study by Bonnefond and Jensen (2012) found that an increase in alpha activity was associated with greater suppression of anticipated distractors in a working memory task, and this power increase was related to individual differences in the ability to suppress distractors. A key question then is why we did not observe a similar trend in our results. Again, the discrepancy in the findings could be due to the task design. In the Bonnefond and Jensen (2012) study, individuals performed a modified Sternberg task in which they were given sequentially presented lists of

letters to memorize. Shortly after the presentation of the letters sequences, distractor items (letters or symbols) were presented during the retention interval of the memory task. Thus, participants were never simultaneously presented both target and distractor items. In our study, both targets and potential distractor items were presented simultaneously, making it inappropriate to suppress all incoming information from the stimulus displays, as was necessary in the Jensen study.

Our results further suggest that alpha-frequency oscillations which reflect working memory gating mechanisms may not be extremely efficient at suppressing continuously changing distractor locations. Work by Thut and colleagues has shown that the suppression of distractors, reflected in alpha frequency synchronization, is fairly location-specific (deGraaf et al., 2013; Rihs, Michel, & Thut, 2007; Romei et al., 2008; Thut & Miniussi, 2009). For example, in these studies, the asymmetry between attended versus unattended locations was a good predictor how much information the participant had about the unattended location. Participants showing the highest alpha power over a particular location were the least likely to have any information about the stimuli presented at that location. An important aspect of many of these studies however is that the distractor versus target locations were always known or fairly predictable. In our task, array items were always displayed at random locations, and in our first experiment, participants freely chose which locations to attend to during every trial. This leaves the possibility that if participants had known which items were targets and which items are distractors, we may have observed a greater increase of alpha activity.

In Experiment 2B, we set out to more directly test whether alpha power is

associated with distractor suppression, determined by an increase in alpha synchronization during distractor-present trials relative to distractor-absent trials. We found no evidence of a significant increase in power during trials that required inhibition. As a matter of fact, we found hints of greater desynchronization during distractor-present trials, indicating that distractors were encoded into VWM in some trials. It may be argued that we failed to find any evidence of distractor suppression because participants did not know ahead of time whether the upcoming trials would contain distractors, and if they had this information we would have found a modulation of alpha power prior to distractors (Bonnefond & Jensen, 2012). However the results of our first experiment, in which participants did have this prior knowledge, makes this postulation unlikely.

The experiments in Chapter II and the current chapter both suggest that alpha desynchronization is related to working memory processing. This again raises the concern that our results conflict with the predictions of the inhibition theory of alpha. However this is not necessarily the case. In all of the experiments so far, visual processing was imperative to performing the task. Consequently, if the inhibition theory only predicts that we should find the suppression of posterior brain regions when they are not functionally relevant to the given task, then it is unsurprising that we do not see any evidence of the disengagement of visual areas.

CHAPTER IV: OBJECTS OR LOCATIONS?

Introduction

In the work so far, we have examined how alpha power is related to visual working memory processing in relation to representing items from a visual display. Our results have shown that as individuals represent more information, there is a graded reduction of alpha-frequency signals, suggesting a desynchronization of neural networks that typically oscillate in this frequency. However what has not been well examined is exactly what about the WM representations the alpha signal reflects. For example, alpha frequency signals may be influenced by what is represented (that is, the features of the represented item), or they may be influenced by the location of the represented items (the spatial location of the items). The experiments in this chapter aim to examine this question.

A long history of attention processing research has shown that attention can operate in two somewhat distinct ways. One is 'object' based and the other 'spatial' based (Duncan 1984; He et al., 2008; Postle & D'Esposito, 1999; Scholl, 2001; Soto & Blanco, 2004). Furthermore, studies on alpha power and attention processing have shown that alpha is considerably influenced by currently task-relevant locations (Gould, Rushworth, & Nobre 2011; Händel, Haarmeier, & Jensen, 2011; Kelly et al., 2006; Rihs, Michel, & Thut, 2007). In our previous experiments, it was difficult to precisely examine what kind of working memory representation alpha reflects because successful performance in all tasks depended on the successful encoding of both location and object information. That is, individuals needed to remember both

the color/orientation of the items and their location.

To test whether the desynchronization of alpha oscillations reflects the number of encoded items or the number of encoded locations, we ran two tasks that manipulated the number of relevant items and the number of relevant locations independently.

Experiment 3A: Sequential Experiment

In our first experiment, we examined whether there is a dissociation between items versus locations representations by presenting the memory set items sequentially. Critically, we varied the number of relevant locations by either presenting sequences of items over the same locations, or different locations. If alpha-frequency oscillations are primarily related to object memory, we should find that the different/same location manipulation should have little influence on the observed level of desynchronization. Conversely, if alpha primarily tracks the number of relevant locations, we should find greater desynchronization when items are presented in different locations relative to the same locations.

Methods

All methods are similar to Experiment 1, except for the following differences.

Participants

23 new participants from the University of Oregon community partook in the experiment. Three subjects were rejected due to an excessive number of EEG artifacts, leaving a sample of 20 participants for the analysis.

Experimental Task

Participants performed a sequential change detection task; a schematic of the experimental task is shown in Figure 12. Each trial could contain 2, 4, or 6 items presented in a sequence of two arrays. Arrays were always evenly split; for example, in a set-size 4 trial, the first array would contain 2 colored squares, and the second array would contain the next two items. Items in the second array could either be presented in the exact same locations as the first two items ('same location' trials), or they could be presented over two new locations ('different location' trials). At test, participants were shown one item (probe), and they had to determine whether the item was part of the memory set arrays. In the same location trials, they had to determine whether this item matched one of the two items shown at that location, while in the different location trials, they had to determine whether it matched the single item shown in the probe location. Each memory array was shown for 150ms, and the two memory arrays were separated by an interval of 1150ms. For the items presented in the first array, this equated to a retention period of 2450ms (1150ms first retention + 150ms second memory array + 1150ms second retention interval). Each trial began with a 500ms baseline period; participants self-initiated each trial by pressing the spacebar. Participants performed 120 trials per set-size/location manipulation, for a total of 720 trials over 20 blocks.

Data Analysis

Behavioral performance was estimated as the average capacity of set-sizes 4 and 6, using Cowan's K estimate (Cowan, 2001). EEG data was again split into trials, and power was estimated using the Hilbert transform. To minimize the amount of

data lost when binning the trial data (total trial time was 3200ms), we changed the analysis window for our statistics to 246ms instead of 236ms.

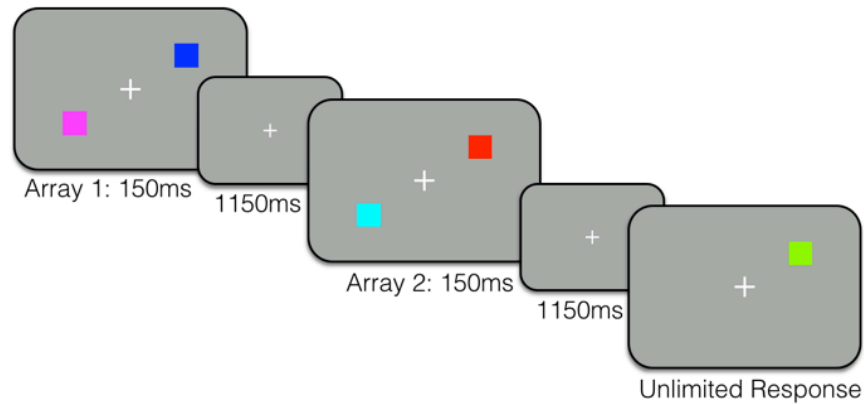


Figure 12: Experiment 3A: Sequential change detection task procedures. Participants saw sequences of two memory arrays; set items were presented in either the same location (shown) or different locations. Following the retention period, participants discriminated whether a probe item matched or did not match items presented at that location.

Results

Behavioral Results

The average capacity for different location trials was 3.12 (SD=0.78), while for the same location trials it was 3.01 (SD=0.72). The difference between these two estimates was not significant ($t(19) = 1.17, p > .05$), and highly correlated ($r = 0.85, p < .01, 95\%CI: [0.66, 0.94]$). Accuracy was significantly higher if the test-probe was part of the second memory array ($t(19) = 4.96, p < .01$); this effect was present in both the different location and same location conditions (all $t(19) > 3.89, p < .01$). Accuracy for the second array did not differ between the location conditions ($t(19) = 0.52, p > .05$).

EEG Results

Alpha power for same and different condition trials are shown in Figure 13A and B. A repeated measures ANOVA on set-size (2,4, or 6), by location (same/different) by time (8 retention period times; 4 following each memory display) revealed significant main effects of set-size ($F(1.21,23.03)=4.78$, $p<.05$), location ($F(1,19)=6.96$, $p<.05$), and time ($F(1.12, 21.22)=11.03$, $p<.01$). The interaction between set-size and location was significant ($F(1.04,19.72)=4.35$, $p=.05$), as was the interaction between set-size and time ($F(3.09,58.66)=3.04$, $p<.05$). For this analysis we constrained the power analysis to just the retention period activity after the presentation of the first and second array since the presentation of the memory arrays lead to an increase of alpha power that was not significantly different from baseline ($F(2.21,43.17)=1.02$, $p>.05$).

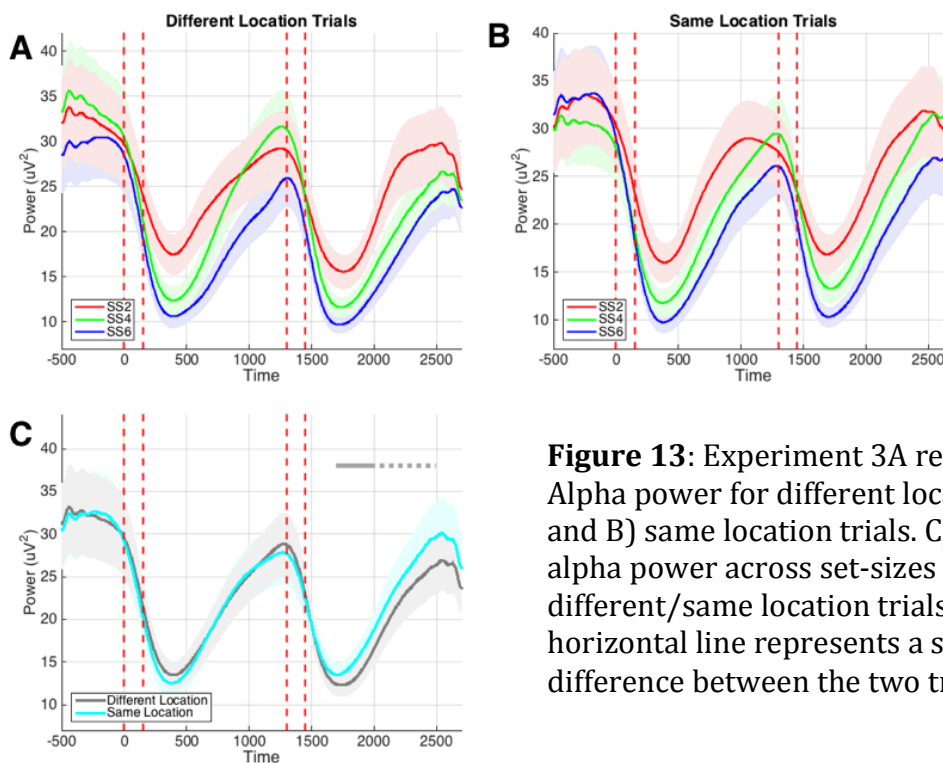


Figure 13: Experiment 3A results. A) Alpha power for different location trials and B) same location trials. C) Average alpha power across set-sizes for different/same location trials. Grey horizontal line represents a significant difference between the two trial types.

Collapsing across set-size location conditions, we found a significant decrease in alpha power after the first memory array (from 238ms to 1222ms) then again after the second memory array (from 1468ms to 2452ms) (all $t(19) > 2.23$, $p < .03^*$); with the exception of the set-size 1 same location conditions, which was only significant until 2206ms following the second array (all $t(19) > 2.25$, $p < .03^*$). Note that this pattern of findings is only significant if we do not correct for multiple comparisons; if we were to use Bonferroni corrected values, no time bins would survive the adjusted alpha level. Contrasts of location condition revealed a significant difference between items presented in the same versus different location ($t(19) = 2.64$, $p < .05$). Examining the difference between same versus different location trials across time, we did not find a significant main effect of condition after the presentation of the first memory array ($F(1,19) = 0.88$, $p > .05$), but the difference was trending in the second retention interval ($F(1,19) = 3.79$, $p = .06$).

Examining the difference between same and different locations across time bins, we found a significant difference between the two conditions primarily in the 1714ms to 1960ms time interval ($t(19) = 2.21$, $p < .05^*$); subsequent time intervals were also marginally significant ($t(19) > 1.80$, $p < .08$), see Figure 13C. Examining this result across set-sizes, we found a difference between same versus different location trials in the same 1714ms to 1960ms time bin interval for set sizes 4 and 6 (all $t(19) > 2.10$, $p < .05^*$), but not set-size 2 ($t(19) < 1.5$, $p > .05$).

Surprisingly, we found a greater reduction in alpha power for same location trials in the 238ms to 484ms time interval (right after the presentation of the first memory array) ($t(19) = 2.81$, $p < .05$). This finding is surprising because participants

did not know ahead of time whether a particular trial would be same- or different-condition trial, and the two conditions were identical during the presentation of the first memory array. However, bordering time bins were not significant (unlike the trend observed after the second memory array), and this effect was only present in set-size 2 condition, suggesting that the finding may be due to noise.

Next, we examined how power in the retention interval following the first and second memory arrays differed between the two location conditions. These results are shown in Figure 14A. In the first retention following the memory array, the same location condition exhibited a substantial increase in power after the second array relative to power decrease after the first array ($t(19)=3.74$, $p<.01$); this increase was also marginally significant in the different location condition ($t(19)=1.84$, $p=0.08$). After this first interval though, the trend between same- and different location conditions diverges. Whereas the different location condition continues to exhibit greater alpha desynchronization relative to the desynchronization observed after the first memory array (all $t(19)>2.6$, $p<.05$ for the 1960ms to 2452ms time bins), the same location condition does not exhibit any substantial increases beyond the desynchronization observed after the first memory array (all $t(33)<1.34$, $p>.05$).

Lastly, we examined if the trend of increased reduction following the second array for the different location conditions depended on accuracy. We found that it did. When examining the accurate only trials, we found the exact same trend of increased reduction in power after the second array. However, inaccurate trials showed an insignificant increase in reduction after the second memory array, similar to the same location trials ($t(19)<0.47$, $p>.05$), see Figure 14B.

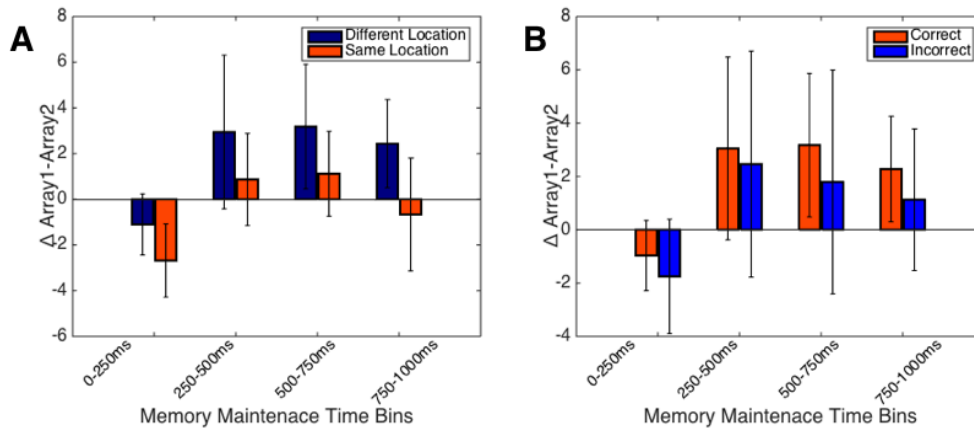


Figure 14: Experiment 3A results. A) Differences in alpha power across consecutive time bins for different and same location trials throughout the retention period. Positive values indicate lower alpha power following the second memory array. B) Difference in alpha power for different location correct and incorrect trials.

Discussion

The results of the current experiment suggest that alpha frequency activity tracks the number of relevant locations instead of the number of relevant items in memory. When items in sequentially-presented memory arrays occupied the same location, we did not observe an increase in synchronization after the second memory array, as would be expected if individuals were representing a greater number of items. However, when items occupied different locations, there was a greater reduction in alpha power after the second array. This effect cannot be explained by individuals being unable to represent a greater number of items in the same-location condition, since accuracy for this condition was equivalent to performance in the different location condition.

A recent report by Manza et al. (2014) has shown that greater

desynchronization in alpha power is observed when the location of relevant items must be updated. Given this finding, an alternative explanation of the current results is that a greater decrease in alpha power in the different location condition represents an updating of the relevant item location representations which is not necessary in our same-location condition. Furthermore, it may be that individuals retain only a few of the items presented in the first array, and mainly concentrate on the items presented in the second array. We have evidence for this possibility by seeing that behavioral accuracy was substantially higher for tested items presented in the second memory array. However, it is important to note that behavior did not significantly differ between the two location conditions, suggesting that though individuals may have misremembered or dropped items from the first memory array, they did so to the same degree in both location conditions.

Experiment 3B: Overlap Experiment

The results of the previous experiment suggest that alpha power is influenced to a greater extent by the number of represented locations rather than the number of represented objects. However, one drawback to the sequential-presentation design is that there are serial order effects, such that individuals are better at remembering items presented toward end of the trial than the beginning. Though the behavioral data did not show a difference between items presented in different or the same locations, it may still be possible that items presented in the same location may have led to some different encoding/updating strategies that were not necessary in the different location condition.

To reduce some of the possible design confounds of sequential-presentation, in our second experiment, we presented all items simultaneously. The main manipulation in this experiment was that in half of the trials, memory array items could overlap, and in the rest of the trials, all items occupied separate locations.

Methods

All methods are similar to Experiment 1, except for the following differences.

Participants

21 new participants from the University of Oregon community took part in the experiment. Two subjects were rejected due to an excessive number of EEG artifacts, leaving a total of 19 subjects for the analysis.

Experimental Task

A schematic of the task design is shown in Figure 15. Participants performed a change detection task with an 'overlap' manipulation. In half of the trials, every two memory array items would overlap. For example, in a set-size 4 trial, two sets of two overlapping items would be shown. The remaining trials were a standard change detection design in which every item occupied a different location. Memory array set-sizes were 2, 4 and 6. To make the overlapping items easier to distinguish, we changed the memory array items to be square outlines instead of filled in squares. Following the presentation of the memory array, participants were presented with a test probe that either matched or did not match one of the items presented in the memory array. If the trial was an overlap trial, participants were asked to

discriminate if the probe matched one of the two items previously shown at that location. Participants indicated their response using a button press. Responses were un-speeded and accuracy was emphasized. Participants initiated each trial by pressing the space bar. Each trial began with a 1300ms baseline period, followed by a 200ms memory array, and 1150ms retention period. Participants performed a total of 120 trials per set-size per location condition, for a total of 720 trials over 20 blocks.

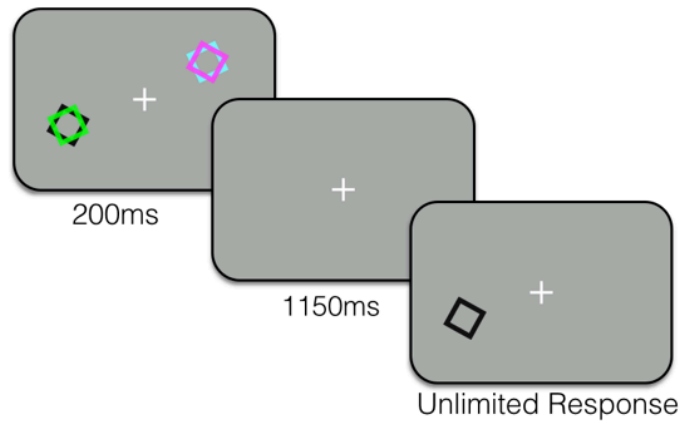


Figure 15: Experiment 3B: Overlap task procedures. Memory array items were presented in either overlapping (shown) or different locations. Following the retention interval, participants indicated whether the probe items was one of the items shown at that location.

Data Analysis

VWM capacity was again estimated using Cowan's K formula (Cowan, 2001). Analysis of the EEG data was based on 244ms time bins, resulting in 11 time-bins per trial. The first and last time bins were discarded from the analysis to avoid edge effects; this resulted in total 9 time bins, 4 time bins were averaged to estimate the baseline activity, 1 time bin (-166ms to 120ms) corresponded to the display of the

memory array, and 4 time bins correspond to the retention period activity.

Results

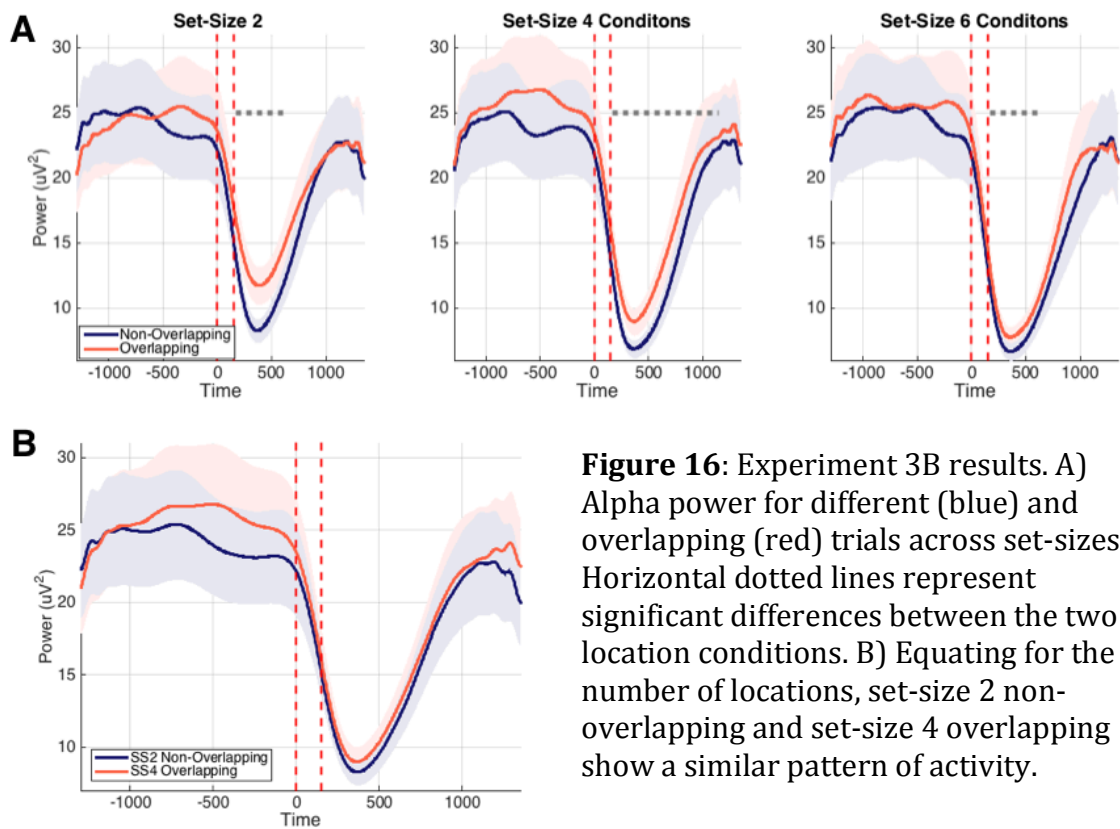
Behavioral Results

Mean memory capacity of the different location conditions was 2.83 (SD=0.86); the mean capacity estimate for the overlapping-location condition was 2.75 (SD=0.75). The difference between the two conditions was not significant ($t(20)=1.20, p>.05$), and the two estimates were highly correlated ($r=0.93, p<.01, 95\%CI:[0.83, 0.97]$). Reaction times (RTs) between the two conditions were not significantly different ($t(20)=0.89, p>.05$); examining RTs by set-size, we found a marginally significant longer reaction time in the overlap condition (versus the different location condition) at set-size 2 ($t(19)=2.09, p=.06$), but not at set-sizes 4 or 6 (all $t(19)<0.94, p>0.05$).

EEG Results

Alpha-power activity for both different location and overlap conditions is shown in Figure 16A. A repeated measures ANOVA of location (different/overlapping) by set-size (2,4,6), by time (4 retention period time bins), revealed significant main effects of location ($F(1,17)=6.74, p<.05$), set-size, ($F(1.08,18.36)=6.91, p<.01$), and time ($F(1.02, 17.28)=5.12, p<.05$). There were no significant interactions. Set-size contrasts showed a significant difference between set-size 2 and 4, ($t(18)=2.65, p=0.05$), set-size 2 and 6 ($t(18)=2.68, p<.05$), and set-size 4 and set-size 6 ($t(18)=2.37, p<.05^*$).

If we examine the difference between set-sizes, split by the location condition, we find that in the different location condition, the average retention-period alpha signal is significantly different between set-sizes 2 and 4 ($t(18)=2.27, p<.05^*$), and trending towards significance between set-size 2 and 6 ($t(18)=1.85, p=0.08$), but is not significantly different between set-sizes 4 and 6 ($t(18)=1.12, p>0.05$). In the overlap conditions, retention-period alpha was significantly different between all set-sizes (all $t(18)>2.74, p<.01$).



Collapsing across location and set-sizes, the difference between baseline power and post-memory array activity became significant after 168ms to 900ms (all $t(18)>2.61, p<.05$); the last time bin (900-1144ms) was trending towards

significance ($t(18)=1.95$, $p=0.07$). Contrasts between the location conditions revealed a significant difference between different and overlapping conditions from 168ms to the end of the trial (all $t(18)=2.17$, $p<.05†$). Breaking this effect even further, we found a significant difference between the set-size 2 overlap trials versus the set-size 2 different location trials from 168ms and 654ms; this timing was the same between set-size 6 trials (all $t(18)>2.30$, $p<.03^*$). For set-size 4 trials, we found a substantial difference between the two location conditions that started at 168ms and persisted until the end to the trial (all $t(18)>2.17$, $p<.04†$).

Next we examined whether the set-size 2 different location trials differed from the set-size 4 overlapping-location trials; the reasoning being that in both of these trial types, the number of attended locations was the same (both had only two locations); see Figure 16B. We didn't find any significant difference between any of the retention period time bins (all $t(18)<1.58$, $p>.05$).

Discussion

Similar to Experiment 3A, we found that the location of working memory representations has a substantial effect on the observed alpha power reductions. When individuals remembered items that were presented in overlapping locations (effectively reducing the number of relevant locations to be represented), we found a decrease in magnitude of the alpha-power reduction. This effect again cannot be explained by individuals remembering fewer items in the overlap condition, since behavior did not substantially differ between the two conditions.

Our finding of no differences in alpha power between set-size 2 different

location and set-size 4 overlapping-locations further suggests that alpha power is primarily related to the representation of locations. In these trials, participants were representing more information in the set-size 4 condition (as evidenced by higher K estimates in this condition), and yet, we found the same degree of power-reduction as in set-size 2 different location trials. In all, the general pattern of alpha power in this experiment supports the conclusion that alpha power reductions reflect the spatial-locations rather than the features of working memory representations.

One possible explanation for the current findings is that individuals grouped the items in the memory array during the overlapping-location trials. This would predict that we should find reaction time difference between the two conditions, since it may take more time for individuals to parse apart grouped representations when presented with the probe item. However, we only found a marginal difference in reaction times at set-size two. This suggests that if there was any grouping, it was not being employed consistently. Of course, given that we emphasized accuracy and not reaction times, it may be possible that reaction time differences may emerge in experimental settings with additional time pressure.

Conclusions

Both the sequential and overlap experiments suggest that alpha power is primarily influenced by the location of represented memory items. In both experiments we found a greater magnitude of alpha reduction when individuals attend to and subsequently recall a greater number of spatial locations. Critically, this effect was not due to participants remembering less information when items were presented in same overlapping locations, since behavior in both experiments

was equivalent to the different location conditions.

These findings support and extend previous research showing that pre-stimulus alpha power greatly influences the probability of being able to detect a difficult target at a specific location (Busch, Dubois, & VanRullen, 2009; Händel, Haarmeier, & Jensen, 2011; Worden et al., 2000). If alpha amplitude reflects the active representation of a particular location, then pre-trial desynchronization, indicating an open gate for input or effectively directed attention to a particular location should greatly impact whether a target is detected or missed.

Furthermore, our results help explain why entrainment through trans-cranial magnetic stimulation (tMS) or repetitive visual stimulation in the alpha frequency is so disruptive to task processing (Capotosto, et al., 2009, 2012; Hanslmayr, Matuschek, & Fellner, 2014; Romei et al., 2008; Silvanto, Muggleton, & Walsh, 2008; Spaak, deLange, & Jensen, 2014). Given that almost all of these tasks required that participants either be able to attend to specific spatial location, or ignore a location that contains distractors, it follows that performance should suffer when the ability to direct spatial attention is hindered through the disruption of alpha oscillations.

In all, these findings suggest that alpha power, and specifically the suppression of alpha power, reflects a mechanism of allocating visuospatial attention and maintaining that information in working memory (Medendorp, et al., 2007; Meltzer, et al., 2008; Palva et al., 2011). Of course, it is difficult to disentangle object information from location information, and in our task, it was necessary to maintain both representations for optimal performance. Further work is needed to more precisely estimate the contribution of spatial versus object information to the

desynchronization of alpha frequency oscillations. For example, it would be interesting to see whether location-based errors, such as swapping or miss-binding of representations is reflected in alpha activity.

CHAPTER V

GENERAL DISCUSSION

Neural oscillations are intimately involved in the representation of behavioral goals and higher-level cognition (Banerjee et al., 2001; Buschman, et al., 2012; Cavanagh & Frank, 2014; Womelsdorf, & Fries, 2007). The main purpose of the current experiments was to examine how neural desynchronization, specifically in the alpha band, is related to working memory. Alpha-frequency oscillations have a well-documented role in working memory processing and have been proposed to be the main mechanism for gating irrelevant information from either entering memory or interfering with items in memory (Foxye & Snyder, 2011; Klimesch, Sauseng & Hanslmayr, 2007; Klimesch, 2012). For this reason, we ran several experiments to examine the modulation of alpha power during visual working memory processing.

In the first experiment, we showed that when participants are performing a visual change detection or whole-report task, we observe a large reduction in alpha activity during the retention period. Furthermore, this reduction is sensitive to set-size, such that the greater the number of items represented, the greater the reduction in alpha power. Importantly, this finding was not a result of differences in our analysis. When we used an analysis path similar to Klimesch and colleagues (2007; Pfurtcheller), we found the same decrease in the magnitude of alpha power with increasing working memory set-size. This finding is inconsistent with the alpha-inhibition hypothesis which predicts an increase in alpha synchronization with increasing memory demands (Sauseng et al., 2005; Waldhauser, Johansson, & Hanslmayr, 2012).

In Experiment 2A, we showed that the observed alpha-power reduction in Experiment 1 is not just a result of the number of items in the memory display. When we held the display size constant and instructed participants to only remember a subset of the items, we found that alpha activity was influenced by the number of remembered items, rather than the number of items in the memory array. In Experiment 2B, we more directly examined the inhibition mechanism that alpha oscillations are thought to reflect by having individuals perform a VWM tasks in which filtering of distractors is undisputedly required. In this task, we again found that the desynchronization of alpha signals fluctuates with the number of items in memory. Critically, we did not find any evidence of increased synchronization in trials which required the suppression of irrelevant distractors. As a matter of fact, we found slightly greater desynchronization of alpha during these trials, possibly indicating a failure to filter the irrelevant items during some proportion of trials.

Given that our first three experiments strongly suggested that the desynchronization of alpha oscillations are related to the maintenance of items in working memory, our last experiments were designed to more precisely examine which aspects of VWM representations the alpha signals reflect. We were specifically interested in examining whether desynchronization reflects the maintenance of object information (for example, features such as color that define the identity of the item), or the maintenance of location information. Using a sequential and overlap paradigm, we found evidence that alpha signals are more strongly related to the location of represented items rather than their features.

Specifically, in both experiments we saw an increase of alpha desynchronization that depended on the number of relevant locations, rather than the number of relevant items.

In general, our findings support the notion that the desynchronization of alpha activity reflects the engagement of cortical regions involved in visual processing. Recent studies recording simultaneous EEG and hemodynamic responses have found a negative correlation between the amplitude of alpha power and BOLD response (Goldman et al., 2002; Logothetis et al., 2001), suggesting that decreases in alpha power reflect the engagement of cortical areas that represents VWM items. Our findings also confirmed work by Okada and Salenius (1998) who found that a sustained decrease in posterior alpha power during a spatial working memory task and later work showing that sustained decreases in alpha power in spatial attention tasks are location specific (Gray et al., 2015; Kelly et al., 2006; Worden et al., 2000).

The question that still remains is why our results conflict with most findings in the alpha and working memory literature. The results of our third set of experiments may provide an answer. Both Jensen et al. (2002) and the studies of Klimesch and colleagues (Klimesch et al., 1999) have found an increase in alpha power with increasing working memory demands. Conversely, studies using either a change detection task or a spatial working memory task have found that the desynchronization of alpha activity occurs with increased working memory load (Gevins et al., 1997; Mendendorp et al., 2007; Palva et al., 2001). A critical trend in these results is that alpha desynchronization is observed when the spatial location of working memory representations matters, and synchronization is observed in

tasks that do not depend on spatial processing. As was shown in Chapter IV, the spatial demands of the current working memory task greatly influenced the amount of alpha power desynchronization that we observed.

The main picture that seems to be emerging from the above results is that alpha oscillations reflect a mechanism of instating which specific neural regions will be recruited during a working memory task. When spatial processing is irrelevant to the working memory task, alpha oscillations seem to reflect the suppression of areas involved in spatial or visual processing (Ergenoglu, et al., 2004; Klimesch, Sauseng, Hanslmayr, 2007; Payne & Sekuler, 2014). However, when the encoding of spatial location is critical to the working memory task, as is often the case with studies on VWM, alpha oscillations reflect the recruitment of areas coding for spatial locations (Mendendorp et al., 2007; Rihs, Michel, & Thut, 2007). Indeed, a recent study by Jokisch, and Jensen (2007) has shown that alpha power is influenced by the recruitment of either ventral or dorsal stream processing, further suggesting that instead of a general inhibition mechanism, alpha-frequency oscillations reflect the recruitment of task-relevant neuronal assemblies (Cohen, 2014; Klimesch, 2012; Palva & Palva, 2007, 2011; Rohenkohl & Nobre, 2011). In all, our findings suggested that alpha-power dynamics are not a unitary phenomenon, rather, the observed levels of synchronization/desynchronization are highly dependent on current cognitive goals.

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