VISUAL WORKING MEMORY REPRESENTATIONS ACROSS EYE MOVEMENTS

by

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DISSERTATION ABSTRACT

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We live in a rich visual world that we experience as a seamless and detailed stream of continuous information. However, we can only attend to and remember a small portion of our visual environment. The visual system is tasked with stitching together snapshots of the world through near constant eye movements, with around three saccades per second. The situation is further complicated with the visual system being contralaterally organized. Each eye movement can bring items in our environment into a different visual hemifield. Despite the many challenges and limitations of attention and the visual system, how does the brain stitch together our experience of our visual environment?

One potential mechanism that could contribute to our conscious perception of a continuous visual experience could be visual working memory (VWM) working to maintain representations of items across saccades. Electrophysiological activity using event-related potentials has revealed the contralateral delay activity (CDA), which is a sustained negativity contralateral to the side of the visual field where subjects are attending. However, how does this work if we are constantly moving our eyes? How do we form a stable representation of items across eye movements? Does the representation transfer over to the other side of the brain, constantly shuffling the items between the

hemispheres, or does it stay in the hemisphere contralateral to the visual field where the items were located when we originally created the representation? The consequences of eye movements need to be examined at multiple levels and time points throughout the process.

The goal of my doctoral dissertation is to investigate VWM representations throughout the dynamic peri-saccadic window. In Experiment 1, I will first compare VWM representations across shifts of attention and eye position. With the focus on the effect of maintaining attention on items across eye movements, Experiment 2 will also explore eye movements both towards and away from attended visual hemifields. Finally, Experiment 3 is designed to substantiate our use of the CDA as a tool for examining VWM representations across eye movements by confirming that the CDA is indeed established in retinotopic coordinates.

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TABLE OF CONTENTS

Chapter Page

LIST OF FIGURES

Figure Page

CHAPTER I

THE IMPACT OF EYE MOVEMENTS ON ATTENTION

INTRODUCTION

We live in a rich visual world that we experience as a seamless and detailed stream of continuous information. However, we can only attend to and remember a small portion of our visual environment. The visual system is tasked with stitching together snapshots of the world through near constant eye movements, with around three saccades per second. The situation is further complicated by the contralateral organization of the visual system, whereby information from one visual hemifield is primarily processed in the opposite cortical hemisphere of the brain. Each eye movement can bring items in our environment into a different visual hemifield and research has explored how the brain keeps track of these changes. Despite the many challenges and limitations of attention and the visual system, how does the brain stitch together our experience of our visual environment?

EYE MOVEMENTS

Eye movements are a complex behavior that is a result of, leads to, and interacts with many cognitive functions, and quite literally have the ability to change our point of view with respect to the world around us. Some researchers have approached this topic by examining visual perception and the eye movements themselves (Sommer & Wurtz, 2008), while others have extended this to the effects of saccades on spatial attention, visual short-term memory, and other cognitive mechanisms (Irwin, Zacks, & Brown, 1990; Hollingworth, Richard, & Luck, 2008; Golomb, Nguyen-Phuc, Mazer, McCarthy, & Chun, 2010). Past single-unit recording literature examined the remapping of receptive fields (Colby, Duhamel, & Goldberg, 1992), while more recent evidence supports converging receptive fields at saccade target locations with implications for attentional facilitation (Zirnsak, Steinmetz, Noudoost, Xu, & Moore, 2014). Spatial updating research continues to investigate pre-saccadic effects (Parks & Corballis, 2008), while other research also suggests lingering memory representations following eye movements (Merriam, Genovese, & Colby, 2003). The field continues to investigate the many peri-saccadic phenomena at the intersection between attention and eye movements.

A separate but related area of research studies the impact of attention on eye movements, including what drives changes of gaze and eye movements in scene perception. However, the present review will focus primarily on the impact of eye movements on attention and visual working memory to help understand how the visual system overcomes various challenges to create our conscious experience of our visual world. In particular, activity in humans will be covered, as well as activity in non-human primates, and other animal, human homologs. First, eye movements themselves will be examined: how are saccades initiated, how does the brain tell the eyes when and where to move, and how is this information organized? Second, the attention and visual working memory literature will be addressed before specifically examining the interaction between eye movements and attention.

Neuroanatomy and physiology of the visual and ocular motor system

At the most basic level, the visual system translates patterns of light on the retina into signals that are interpreted as our visual experience. However, our eyes are not always fixed in space. The human visual system has evolved to perform visually guided eye movements to locate objects in space, which requires a complex interplay of many brain structures to coordinate the areas that process the incoming information and produce the eye movements (Schall, 2009). Visual input from the retina goes through the lateral geniculate nucleus (LGN) and superficial layers of superior colliculus to transmit the information to visual cortex and then on to parietal, including lateral intraparietal area (LIP), and temporal cortices before reaching the fontal eye fields (FEF) (Schall, 2009). FEF plays an important role in saccade production and oculomotor systems. It has projections to various relevant areas and is innervated by many others, including strong interconnectivity with extrastriate visual cortex. FEF is further connected with dorsolateral prefrontal cortex (DLPFC) and supplementary eye field (SEF), and feeds into the saccade generator through intermediate layers of the superior colliculus, basal ganglia through ipsilateral striatum, and the cerebellum through the pontine nuclei of the brain stem (Schall, 2009). The role of FEF in producing saccades was originally suspected when electrical stimulation in one FEF hemisphere in macaques caused contralaterally directed saccadic eye movements (Schall, 2009). Such stimulation across FEF evokes saccades of gradually varying direction and amplitude, providing early insight into how saccades are generated (Schall, 2009). At any given moment each of these specialized areas of the visual system must process information projected from previous parts of the processing stream and provide inputs to further processing, while interacting with near and far-reaching corticies. This is an impressive process when the eyes are not rapidly scanning the visual world; however, matters are further complicated when eye movements are taken into account.

Eye movements: motor planning and mechanics

Saccades

Processing a complex visual scene may require several eye movements to bring potential visual targets over the high-resolution of the fovea for inspection (Pertzov, Avidan, & Zohary, 2011). In fact, such eye movements are necessary to our visual experience as demonstrated when perfect fixation is maintained, the visual system quickly adapts to the present visual stimulation and everything fades away from our view (Martinez-Conde, Macknik, & Hubel, 2004). Saccades, where the eyes rapidly move between two resting positions, can cause dramatic shifts to the position of the images projected on the retina, even when the items represented remain at fixed positions in space (Ross, Morrone, & Burr, 1997). Although this will be addressed in more detail later, this is a key issue that the brain must resolve to give us a stable perception of the world. The brain must keep track of the current state of the eyes, plan the next eye movement, determine when or if the eye movement plan should execute, and predict how this eye movement plan will impact the placement of the retinal image.

Motor level

At the motor level, saccades are produced by burst and motor neurons that innervate extraocular motorneurons that provide the force to rapidly rotate the eyes, which is counteracted by a second amount of force from tonic neurons to maintain eccentric gaze (Schall, 2004a). The saccade generator, located in the brainstem, ultimately receives the command when it is time to move the eyes and where they should then re-fixate (Schall, 2004a). Past research has shown that visually guided saccades can be made reflexively, while saccades toward targets (pro-saccades) tend to be generated faster than saccades away from targets (anti-saccades) when a cue must be evaluated (Clementz, Brahmbhatt, McDowell, Brown, & Sweeney, 2007). Anti-saccades also differ from pro-saccades by recruiting greater prefrontal cortex (PFC) activity (Clementz, Brahmbhatt, McDowell, Brown, & Sweeney, 2007), as well as activity in other areas of the oculomotor circuit (O'Driscoll, Alpert, Matthysse, Levy, Rauch, & Holzman, 1995). Areas involved in voluntary saccades include FEF, SEF, the parietal eye field (PEF), and precuneus in superior parietal cortex, while striate and extrastriate cortices help guide visuomotor responses related to stimulus processing (Clementz, Brahmbhatt, McDowell, Brown, & Sweeney, 2007).

The pre-saccadic time period involves changes of activity in many brain areas. In particular, single unit recordings in area LIP in rhesus monkeys showed enhanced sensory responses to the spatial locus of a given receptive field for a covertly attended stimulus as well as for one that will be representing the target of a future saccade (Colby, Duhamel, & Goldberg, 1996). Specifically, the researchers saw increased visual responses to stimuli presented, regardless of behavioral relevance, during a memory guided saccade task (Colby, Duhamel, & Goldberg, 1996). The responses of LIP neurons were related to sensory processing but were also subject to cognitive factors, such as attentional modulation, and were related to motor planning and saccade production (Colby, Duhamel, & Goldberg, 1996). The various changes that the visual system undergoes in preparation for an eye movement suggests its high priority in visual processing.

Tracking where the eyes need to move

In regards to where the eyes need to be moved, research has identified multiple reference frames for saccades. Oculomotor space and saccade amplitude have been mapped out across the lateral bank of the intraparietal sulcus (IPS) contralateral to the direction of the eye movement (Savaki, Gregoriou, Bakola, Raos, & Moschovakis, 2010). This further enforces the contralateral organization of the visual system as a whole. Functional magnetic resonance imaging (fMRI) has additionally revealed that saccades of equal amplitude are represented within a retinotopic reference frame in FEF and IPS in human cortex (Pertzov, Avidan, & Zohary, 2011). However, saccades to a common target, despite having different movement vectors, also revealed spatiotopic representations in the middle aspect of IPS (Pertzov, Avidan, & Zohary, 2011). The study further suggested that eye movements are made both in egocentric and allocentric representations of space and implicated parietal cortex in maintaining our representations of space across these various reference frames (Pertzov, Avidan, & Zohary, 2011). Areas in multiple corticies are recruited to keep track of upcoming saccade targets.

In non-human primates LIP neurons fire after a visual target is presented and just before a saccade is initiated to that target, as well as sustained activity between the time points (Schluppeck, Glimcher, & Heeger, 2005). In a typical memory-guided or delayed saccade task, the subject is cued to fixate centrally before a target is presented in the periphery for a brief period of time. The subject must maintain central fixation until cued to then make a saccade to the remembered location of the peripheral target (Schluppeck, Glimcher, & Heeger, 2005). Similar to activity seen in LIP and the parietal reach region (PRR) in macaques, memory-guided saccade tasks with humans using fMRI have shown characteristic sustained activity during the delay-period in visual area 7 (V7), and intraparietal sulcus 1 (IPS1) and 2 (IPS2) (Schluppeck, Curtis, Glimcher, & Heeger, 2006). The delay period activity was also strongly lateralized with greater activity contralateral to the target's visual field providing evidence for similar topographic mapping in human parietal cortex (Schluppeck, Curtis, Glimcher, & Heeger, 2006). Other research has plotted the responses to remembered target angles and found that these positions are held in retinotopic reference frames (Sereno, Pitzalis, & Martinez, 2001). These topographic maps in human parietal cortex can help keep track of where the eyes intend to move to next.

Determining when or if the eyes need to move

In regards to when a saccade must be performed, a plan must first be created, and visual information that helps guide the saccades to their next target must be processed. Posterior parietal cortex (PPC) is implicated in sensorimotor integration between visual and motor areas to help us bring in and act on visual information (Van Der Werf, Buchholz, Jensen, & Medendorp, 2009). Evidence has shown high-frequency neuronal synchronization in PPC in humans during saccade end point planning, which may suggest temporal coding as a method for maintaining the goal of a saccade in mind until it can be executed (Van Der Werf, Buchholz, Jensen, & Medendorp, 2009). Such synchrony may also facilitate the interactions between disparate areas of cortex in planning saccades and warrants further research.

At the lowest level, saccades are generated by pulse-step activity in motor neurons, with the various features of the stimulation determining the ultimate features of the eye movement itself (Crawford & Muller, 1992). The velocity of the eye movement is determined by the neural burst frequency of the pulse generator, while the amplitude of the saccade, meaning the distance that the eyes move, is determined by the burst duration (Crawford & Muller, 1992). Some degree of variability exists in this system that encompasses potential errors, which leads to the need for corrections in saccades (Crawford & Muller, 1992).

Once a saccade is planned up it can take a latency of 50ms to cancel the plan if a ‘stop’ cue is presented (Schall & Thompson, 1999). Related to the cancellation or withholding of saccades, single-unit recording investigated the different populations of neurons in supplementary motor area (SMA) and FEF in Rhesus monkeys (Schall, 1991a; Schall 1991b). No-go-specific cells in SMA showed preferential activity when a withheld saccade would have targeted an item in the contralateral visual hemifield (Schall, 1991a). Even though the saccade was not performed, the fact that a saccade had been planned allows the visual system to still catalog information about the location of the potential saccade target (Schall, 1991a). During the pre-saccadic period when the saccade plan will eventually be executed, some cells in FEF and SEF begin to fire, but after the saccade is initiated activity in SEF ceases, while activity in FEF continues until the saccade is completed (Schall, 1991b). A further difference in activity between these areas is that neurons in SEF more strongly code for current eye position than those in FEF (Schall, 1991b). Having these processes dedicated to what happens when a saccade plan is cancelled or withheld from execution suggests that the visual system has developed to tackle all of the changes it must make when saccades are carried out.

Corollary discharge

With initiating saccades and setting eyes into motion, the brain needs to compensate for and anticipate the eventual change in visual input. Many theories of spatial remapping, discussed in more depth later, require the transfer of visual information from neurons, which code a target before the saccade, to those neurons that will encode the same area of space following the eye movement. Research has shown that passive displacement of the eye results in a shift of the visual world, while voluntary movement of the eye does not (Bridgeman, Van der Heijden, & Velichkovsky, 1994). This observation suggests a key role of keeping track of pending eye movements in our perception of a stable visual world (Colby, Berman, Heiser, & Saunders, 2005). One method for this may be corollary discharge, which is an internal copy of the eye movement signal sent in parallel to the oculomotor command for the motor neurons (Colby, Berman, Heiser, & Saunders, 2005). One potential pathway for the corollary discharge signals between visual hemifields and cortical hemispheres involves the forebrain commissures (Colby, Berman, Heiser, & Saunders, 2005). More recent research traces the pathway through superior colliculous and the medial dorsal nucleus of the thalamus to FEF to allow the frontal cortical neurons to alter their activity to match up with the displaced visual input (Sommer & Wurtz, 2008).

What eye movements can tell us about underlying and related processes

Saccadic suppression

Various changes in visual information processing and cognition, including latency and topographical differences, occur with saccades as revealed by electroencephalography (EEG) in humans (Skrandies & Laschke, 1997). During a saccadic eye movement the stream of visual input is briefly interrupted, with reduced visual sensitivity, while items are rapidly shifted to new retinal locations; however, we are largely unaware of these near constant shifts (Collins, Rolfs, Deubel, & Cavanagh, 2009). The brain suppresses conscious awareness of the movement itself, while masking this potential gap in perception (Collins, Rolfs, Deubel, & Cavanagh, 2009). Psychophysical evidence points to saccadic suppression influencing magnocellular thalamic neurons, while fMRI in humans shows neural correlates of saccadic suppression in both dorsal and ventral streams (Kleiser, Seitz, & Krekelberg, 2004).

Further insights

Consistent with the reafference principle, research suggests that a copy of the oculomotor signal that indicates self-generated motion of the eyes, along with sensory input, help compensate for the shifts of the retinal images so that we only perceive motion in our environment when the items themselves move (Kleiser & Skrandies, 2000). Supporting evidence comes from the differences observed in brain activity during a saccade versus when the eyes remain fixated. The visual system performs computations taking into account the relative velocities of the stimulus and eye (Klesier & Skrandies, 2000). The brain must therefore reconcile where items are located in space with their projections onto the retina, as well as take into account the current state of the eyes (Klesier & Skrandies, 2000).

Systematic mislocalization errors observed when an item is briefly presented before or during a saccadic eye movement suggest changes in how space is processed around the target of the saccade (Kaiser & Lappe, 2004). These mislocalizations suggest that space around the saccade target is compressed whereby mislocalizations closer to fixation shows uniform shifts consistent with the saccade direction, while stimuli presented in the distant periphery are often perceptually mislocalized orthogonal to the direction of the saccade (Kaiser & Lappe, 2004). The shifts of the reference points and the eventual compression of perceptual space must be evaluated in the peri-saccadic time period (Kaiser & Lappe, 2004). If these processes take different amounts of time, this may help explain why mislocalizations occur (Kaiser & Lappe, 2004). The potential issues with such variability in the system are likely reduced at relevant points in space by attention shifting from the current point of fixation to the saccade target before the saccade is initiated, facilitating visual processing at these target locations (Kaiser & Lappe, 2004).

Using tasks where a saccade target is shifted, between the time when the saccade is initiated and when the eyes land, offers an opportunity to examine how the visual system codes location across saccades (Collins, Rolfs, Deubel, & Cavanagh, 2009). If the computations necessary for performing the eye movement were exact, we would expect to see the saccade land at the pre-saccadic target location. However, some degree of error in saccade landing points suggests errors in the system. These errors likely reflect variability in the efference copy vector compared to the saccade vector. Judgments of the displacement between the pre- and post-saccadic targets can be used to investigate how the visual system can track the original pre-saccadic target location (Collins, Rolfs, Deubel, & Cavanagh, 2009). Such discrimination tasks about the direction of displacement provide evidence for egocentric spatial location processing where the efference copy is important to remapping the location of the pre-saccadic target in post-saccadic retinotopic coordinates (Collins, Rolfs, Deubel, & Cavanagh, 2009).

Going back to the role that attention can play in easing the transition of visual processing at the original fixation point and at the location of the saccade target, some studies have investigated differential shifts of the eyes as well as attention. Event-related potentials (ERP) in humans, time-locked to the onset of the saccade, reveal separable components for shifting attention to the stimulus, for further enhancement when this stimulus is also the target of the impending saccade, and for the signal related to saccade initiation (Wauschkuhn, Verleger, Wascher, Klostermann, Burk, Heide, & Kompf, 1998). However, it is clear from the eye movement literature that it is difficult to disentangle eye movements and attention with their interactions in facilitating visual processing and that some form of transient visual memory is necessary to perform simple perception and orienting across eye movements (Hollingworth & Ramussen, 2010).

ATTENTION

With countless objects in our visual environment, not even taking into consideration our near limitless internal thoughts, our brain is tasked with identifying a smaller subset of items that we can actually process at any given time. The mechanism by which we filter, focus, and prioritize these items is attention. However, attention is a broad field in and of itself. Therefore, I will be focusing on visual attention, and its complimentary and overlapping cognitive process, visual working memory (VWM).

Attention, meaning the locus of attention and the preferential processing at that location, can be described by attentional facilitation. Behaviorally, attentional facilitation can be operationally defined as increased accuracy or reduced response times when an item in an attended area is probed. At the neuronal level, attentional facilitation can then be quantified as the increased firing rate for neurons whose receptive fields contain the attended item (Gregoriou, Gotts, Zhou, & Desimone, 2009). Research has shown these enhanced firing rates in FEF and visual area 4 (V4) as well as oscillatory coupling between the regions in the gamma frequency band (Gregoriou, Gotts, Zhou, & Desimone, 2009). This coupling suggests top-down effects of FEF on V4 in tasks that require spatial attention and bottom-up effects of V4 on FEF when sustained attention is required (Gregoriou, Gotts, Zhou, & Desimone, 2009). More generally, FEF in monkeys and humans has been shown to be involved in covert attention, where attention is directed to a location other than where the eyes are fixated (Gregoriou, Gotts, & Desimone, 2012). This provides a simple demonstration that although attention and gaze are intrinsically related, it is possible to focus attention away from where the eyes themselves are focused.

Zooming out to scalp level, ERP recordings have allowed researchers to investigate the mechanisms of attention in humans. Such studies have shown that attention can have early effects in the visual processing stream, both in voluntary attention and automatic attentional capture contexts (Luck, Woodman, & Vogel, 2000). ERPs have helped address the hotly debated topic of whether attention operates at an early sensory or later stage once a stimulus has already been perceived (Luck, Woodman, & Vogel, 2000). Research shows evidence for attentional modulation as early as 60ms following the onset of the stimulus, when visual information is just entering extrastriate visual areas (Luck, Woodman, & Vogel, 2000). This evidence points to the impact attention can have on our visual experience, operating at such an early stage of visual processing. Depending on task demands, attention can shift between objects or locations in as quickly as 100ms or take several hundred milliseconds (Luck, Woodman, & Vogel, 2000).

Attention and visual working memory

When attention is sustained or when the attended stimuli are no longer in view, the research field boundaries begin to blur with those of memory. This will become more important when considering where mental representations of visual items are held during a saccade. Memory can be divided into long-term and short-term memory, where short-term memory can then be further divided into verbal and visual storage. This visual short-term, or working, memory has a limited capacity of only three to four items and holds items in an easily accessible format (Luck & Vogel, 1997). These items can have as many as four features each, including color and orientation (Vogel, Woodman, & Luck, 2001) and participants can control which features they selectively store in VWM (Woodman & Vogel, 2008). Much research has examined the binding of these features to a single object representation (Hollingworth & Ramussen, 2010).

A standard task used to measure VWM capacity is the change detection paradigm, which draws on the findings from change blindness studies that illustrated humans' limited capacity to detect changes between serially presented complex visual displays (Luck & Vogel, 2013). In a standard change detection task the participants are presented with an array of colored squares for a brief period of time, followed by a blank retention interval, and then a test where the colored squares are presented either all identical to the original memory array, or with one item changed in color at one of the previous locations (Luck & Vogel, 2013). Participants then indicate whether the two arrays are the same or different. By manipulating the number of items in the arrays and taking into account any inflation to accuracy from guessing it is possible to calculate an individual's VWM capacity with the equation $K = S(H - F)$ (Vogel, McCollough, & Machizawa, 2005). In this equation, K is an individual's VWM capacity estimate, S is the number of items presented in the memory array, H is the hit rate where participants correctly identified a change between the displays, and F is the false alarm rate where participants incorrectly responded that a change occurred when one did not (Vogel, McCollough, & Machizawa, 2005).

Contralateral-delay activity

Turning once again to ERPs, researchers found lateralized activity in humans (Vogel & Machizawa, 2004), and later a homologous component in macaques (Reinhart, Heitz, Purcell, Weigand, Schall, & Woodman, 2012), that tracks visual working memory maintenance during the delay period between the onset of the memory array and the test. In humans, this is seen as a sustained negativity at posterior electrode sites, contralateral to the visual hemifield that is being attended (Vogel & Machizawa, 2004). The amplitude of the component increases as a function of the number of items being held in memory up to an individual’s VWM capacity (Vogel & Machizawa, 2004). This component is referred to as the contralateral delay activity (CDA) and is sensitive to individual differences in VWM capacity, filtering efficiency when targets and distractors are present, and when adding or excluding items from memory (Vogel & Machizawa, 2004; Vogel, McCollough, & Machizawa, 2005). This activity cannot be explained by increased illumination by more items at higher set sizes being presented on the screen, nor contamination from microsaccades or load dependent eye movements, but is instead directly tied to an individual’s behaviorally measured VWM capacity (Vogel & Machizawa, 2004; Kang & Woodman, 2014).

Individuals with higher visual working memory capacity estimates are not only capable of holding more items in memory, but are also more efficient at maintaining only target stimuli in memory while ignoring distractors (Vogel, McCollough, & Machizawa, 2005). This is clearly seen in the CDA, as the ERP difference waves between the contralateral and ipsilateral activity, where the amplitude for maintaining two items is the same as when maintaining two items when two distractors are present, while a substantial increase in amplitude occurs when four items are being maintained (Vogel, McCollough, & Machizawa, 2005). In contrast, low VWM capacity individuals showed a similar CDA in the two target with two distractor condition as was seen in the four item condition, suggesting that the participants were not able to efficiently filter out the distractors (Vogel, McCollough, & Machizawa, 2005).

Interestingly enough, highlighting the overlap in sustained attention and visual working memory, the CDA, as a measure of cognitive load, can be obtained in a task where the stimuli do not disappear during the retention interval. Instead the items can remain on the screen while the participants actively monitor the items until the test when they must make a two-alternative forced choice response to a test probe in the attended visual hemifield (Tsubomi, Fukuda, Watanabe, & Vogel, 2013). The results show the same behavioral estimates of VWM capacity, K, as well as a comparable CDA, including the asymptote correlated with individual differences, seen in a standard change detection task (Tsubomi, Fukuda, Watanabe, & Vogel, 2013).

Attentional tracking

Further investigation of sustained attention led to studies in attentional tracking. After allocating attention to a stationary object in our visual environment, how then do we keep track of the item once it starts to move while our eyes remain fixed? Attention can be divided to track up to four simultaneously moving target items, even amongst distractors (Alvarez & Cavanagh, 2005). In our constantly changing visual environment, the visual system must keep track of relevant items amongst irrelevant items, which will only become further complicated once the eyes also start to move. However, when the eyes remain fixated, research has examined how we are capable of overcoming such challenges. Tasks where participants were instructed to attend to a bar of a spinning pinwheel showed separable tracking resources in each of the visual hemifields (Alvarez & Cavanagh, 2005).

The versatile and robust CDA was also used to examine individual differences in attentional tracking ability to moving objects in a multiple object-tracking (MOT) task (Drew & Vogel, 2008). In a modification of a change detection paradigm, participants were presented with an initial cue array of squares where 1, 2, or 3 targets were highlighted with a color before all of the items became black (Drew & Vogel, 2008). The items moved around in the attended visual hemifield on the screen during the retention period before stopping and one of the items was probed in the test array where the participant had to indicate if the item was one of the originally highlighted items in the cue array (Drew & Vogel, 2008). To perform this task while remaining fixated, participants would have to covertly attend to the locations of the target items to be able to correctly identify the target items amongst the distractors following the motion phase (Drew & Vogel, 2008). Looking at the contralateral, negative going waves the N2pc component occurred around 200ms following the onset of the cue array and showed graded amplitude increases with the number of targets that were selected by attention (Drew & Vogel, 2008). The CDA showed sustained activity with amplitude sensitive to the number of targets being tracked and reflected individual differences in attentional tracking capacity (Drew & Vogel, 2008).

Perceptual and cognitive processes in a spatial reference frame

Attentional tracking underscores the importance of the spatial reference frames in perception and cognition in the visual modality. When items are briefly hidden from view or move throughout distractors in the environment, how does our brain match up the mental representation of the item in its current position with that where it was first encoded? What kind of coordinate system does the visual system use to maintain an item's identity, binding its features together despite appearing in different locations?

Spatial perception

Starting at a more basic level, how do we perceive the location of stationary items? fMRI studies in humans have shown the use of egocentric reference frames, meaning with respect to where the observer is located, for both visual and somatosensory stimuli in PPC and associated frontal regions (Galati, Pelle, Berthoz, Committeri, 2010). Egocentric reference frames are particularly useful when the observer is acting on the objects in the environment or is receiving proprioceptive feedback or motor efference copies (Galati, Pelle, Berthoz, Committeri, 2010). Other brain areas, including parahippocampal and retrosplenial regions, and the precuneus, use persistent cues within the environment to orient objects within allocentric reference frames, meaning with respect to the environment (Galati, Pelle, Berthoz, Committeri, 2010).

It was previously assumed that a spatiotopic reference frame would be necessary to stitch together our conscious perception of a seamless environment, rather than purely perceiving our environment through retinotopic coordinates that would change with every eye movement. At the earliest levels of the visual system it makes sense that stimuli are encoded in retinotopic space where each area of light that falls on the retina corresponds to a specific part of the incoming image. However, the mechanisms by which we experience contiguous space remain more illusive. At which point could higher cognitive areas interpret these lower level signals in the context of the present scene? fMRI in humans has found stimuli representations in retinotopic coordinates in areas as high in the visual processing stream as cortical area MT (middle temporal), as was found in the homologous area in monkeys (Gardner, Merriam, Movshon, & Heeger, 2008). The researchers further suggested that this was also the case for all of occipital cortex that is visuotopically organized, although noting a few exceptions in the literature (Gardner, Merriam, Movshon, & Heeger, 2008).

One such study found evidence for head-based receptive fields in lateral occipital complex (LOC) that would be more stable across eye movements (McKyton & Zohary, 2007). The location of items were shifted either in space on the screen or by changing the subject's eye position, which resulted in adaptation effects when the position of the items on the screen remained constant even if the position on the subject's retina changed (McKyton & Zohary, 2007). LOC in the hemisphere contralateral to the presented item also showed greater activation (McKyton & Zohary, 2007).

Further evidence suggests a gradient from strictly retinotopic coordinates in primary visual area (V1) to integrating more spatiotopic coordinates along the ventral stream into area V4 and inferior temporal (IT) cortex, whereby the position of the eyes works to modulate receptive field activity (McKyton & Zohary, 2007). Research in monkeys has also investigated this interaction between reference frames in the dorsal stream (Duhamel, Bremmer, BenHamed, & Graf, 1997), while further evidence in ventral intraparietal (VIP) area in head-fixed monkeys has identified head-centered coordinates (as cited in Gardner, Merriam, Movshon, & Heeger, 2008; Colby & Goldberg, 1999).

Spatial attention

Briefly considering the role of attention in driving eye movements, it is important to mention the premotor theory of attention that suggests biases in covert spatial attention by pending oculomotor plans (Thompson, Biscoe, & Sato, 2005). Although we can passively perceive visual input, we often examine the space around us with particular goals in mind, including the intention to act and involve the motor system, or of primary relevance here, to bring something into clear focus by directing our eyes to a relevant target. Parietal cortex is important in encoding representations of objects in our environment in egocentric reference frames that would allow for future action by the observer (Colby & Goldberg, 1999). To assist with transformations from sensory to motor signals, neurons in parietal cortex are modulated by both top-down and bottom-up attention, which can help the observer select the target (Colby & Goldberg, 1999).

The single-unit recording literature has frequently used tasks that include fixation, peripheral attention, and delayed saccades in an attempt to disentangle the enhanced activity seen in the peri-saccade period as either attentional, meaning related to attention, or intentional, meaning related to the intention to make an eye movement or otherwise act on the target (Colby & Goldberg, 1999). The saliency of the stimulus appears to ultimately modulate the responses of neurons in LIP, without a further motor plan, eye movement, or other behavioral response being necessary (Colby & Goldberg, 1999; Thompson, Biscoe, & Sato, 2005).

Spatial working memory

Moving into spatial working memory, it can be difficult to disentangle visual working memory for visual items that are perhaps inherently tied to their locations in space where they were encoded, and spatial working memory, which focuses more on the locations themselves. However, studies in macaques and humans have found recruitment of a vast number of areas in oculomotor and mnemonic processing, including activity in extrastriate cortex (Berman & Colby, 2002). Single-unit recording in macaques found delay period activity in memory-guided saccade tasks in extrastriate visual cortex (Berman & Colby, 2002). On top of higher-order association areas (e.g. PPC, FEF, SEF, and PFC) fMRI studies using memory-guided saccade tasks also found significant activation in extrastriate cortex in humans, specifically in the posterior superior temporal sulcus (PST) and lateral occipitotemporal cortex (LOT) (Berman & Colby, 2002).

Spatial updating

Now that we have reviewed eye movements, visual processing, attention, and working memory occurring within spatial reference frames, we can start to identify how each of these components interacts to create our conscious perception of our visual world. For now, how do we keep track of where objects are located even when we, the observer, are moving? The spatial updating literature has investigated how our brains compensate for observer movements including saccades, smooth pursuit eye movements, as well as whole-body rotations and translations (Klier & Angelaki, 2008). Research has focused on the integration of oculomotor, motor, vestibular, and somatosensory signals with visual processing to keep track of the voluntary motion produced by the observer and how this impacts the visual input (Klier & Angelaki, 2008). This information is then used to impact responses at the neural level in how we process further visual inputs (Klier & Angelaki, 2008). Magnetoencephalography (MEG) in humans has revealed rhythmic neural synchronization in PPC to help emphasize which reference frames are task-relevant for current spatial processing (Van Der Werf, Buchholz, Jensen, & Medendorp, 2013). Research has shown the importance of gaze direction, which includes eye and head angle, in spatial updating that is solidified in early development including the relevance of gaze direction in individuals who developed blindness later in life (Reuschel, Rösler, Henriques, & Fiehler, 2012). However, spatial updating at the neural level shows that changes in activity in LIP in macaques are potentially independent of the direction of the saccade (Heiser & Colby, 2006).

Studies of spatial updating with regards to saccades have used the double-step task to investigate the particular timing of potential updating between eye movements (Bellebaum, Hoffmann, & Daum, 2005). Such studies of spatial updating across saccades in humans using ERPs examine the activity time-locked to the onset or offset of the saccade (Bellebaum & Daum, 2006; Bellebaum, Hoffmann, Daum, 2005; Peterburs, Gajda, Hoffmann, Daum, & Bellebaum, 2011). Such research has implicated PPC in spatial updating and suggests that updating does not occur until 150ms after the first saccade is initiated, giving the visual system time to integrate information about the first eye movement with motor information about the second pending saccade (Bellebaum Hoffmann, & Daum, 2005). The authors suggest that the differences in timing they find are related to their task reflecting the updating of motor coordinates rather than maintaining stimulus locations in memory across saccades (Bellebaum, Hoffmann, & Daum, 2005).

EYE MOVEMENTS AND MEMORY/TRANS-SACCADIC MEMORY

Having previously addressed how we move our eyes and then how we can attend to and remember items in our environment when our eyes are stable, even if the items are moving, what happens at the intersection between eye movements, attention, and visual working memory, at a more in-depth level? Going back to the potential challenges posed by saccades, including saccadic suppression, how do we hold onto relevant items across eye movements? When saccadic suppression was addressed above, it was suggested that some form of attention or memory might be necessary to fill in the gap between one fixation and the next (Luck & Vogel, 2013). This is the territory of trans-saccadic memory, where attention and working memory play a vital role in maintaining our visual experience during the dynamic peri-saccadic period.

The intention to make an eye movement impacts many other cognitive processes, alerting various cortical areas to hold onto whatever they are currently doing so that it can then be compared to and matched up with new inputs of the same items following the saccade. These effects can be seen both when the saccade is fully executed and, to a lesser extent, when the saccade is planned but ultimately withheld, such as in a go/no-go task (Geng, Ruff, & Driver, 2009). Early theories of 'trans-saccadic integration' suggested that information across eye movements was essentially overlapped so that the brain somehow combined the pre- and post-saccadic input to create one conscious percept (Irwin, Brown, & Sun, 1988; Irwin, Zacks, & Brown, 1990; Melcher & Colby, 2008). However, this proved not to be the case. Instead, visual short-term memory (VSTM), or VWM, has been proposed as an ideal mechanism to hold onto visual information while the retinal coordinates of a visual target are displaced across a saccade (Melcher & Colby, 2008). Although sharing many of the defining characteristics of VSTM and VWM, this storage space is sometimes alternately referred to as a separate cognitive phenomenon, such as trans-saccadic perception (TSP) or simply trans-saccadic memory, as it is memory only with relation to saccades (Prime, Vesia, & Crawford, 2011). Others have also described trans-saccadic memory as VSTM plus an additional visual analog that holds onto attended and non-attended items across the saccade (Germeys, Da Graef, Van Eccelpoel, & Verfaillie, 2010).

VSTM has also been shown to play a reciprocal role in influencing gaze correction following an errant saccade trajectory by helping the visual system reacquire the original goal-relevant target (Hollingworth, Richard, & Luck, 2008). Participants were asked to make a saccade from a central fixation cross to a target on an outer wheel of potential stimuli that sometimes rotated and required the participant to make corrections in their eye movement to eventually land on the correct target (Hollingworth, Richard, & Luck, 2008). VSTM helped create object correspondence across the eye movement, which led to fast, efficient, and accurate saccade correction (Hollingworth, Richard, & Luck, 2008). A concurrent visual working memory task that would load VSTM had detrimental effects on saccade correction, providing further evidence of VSTM's role (Hollingworth, Richard, & Luck, 2008).

This trans-saccadic memory for items can be disrupted using single pulse transcranial magnetic stimulation (TMS) applied over PPC (Prime, Vesia, & Crawford, 2008). TMS proved most disruptive when participants were asked to remember the orientation of tilted Gabor patches following a saccade, especially when the pulse was applied over right PPC in time with saccade initiation (Prime, Vesia, & Crawford, 2008). While the participants had previously been able to hold three to four Gabor patches in memory, the researchers found a temporary TMS-induced effect whereby participants' capacity reduced to reporting the features for only one Gabor patch (Prime, Vesia, & Crawford, 2008).

Despite the saliency of spatiotopic coordinates in our daily lives, especially with visually guided behaviors, research has found that memory is far more accurate and accumulates fewer errors across saccades when held in the original retinotopic coordinates of the visual system (Golomb & Kanwisher, 2012). In a VWM continuous color report task, participants have also shown biased errors towards distractor stimuli that appeared at the retinotopic location of a previously displayed cue following a saccade (Golomb & Kanwisher, 2014). The biases in the response distributions showed smaller errors, consistent with mixing of the correct target color and the distractor color, as well as larger errors, consistent with swapping of the memory representation for the distractor color (Golomb & Kanwisher, 2014). This result suggests errors in fully shifting attention to the new retinotopic location of the attended target.

Eye movements and attention

Attention plays an important role before and after the eye movement. Research shows that before a saccade is even initiated, attention is covertly shifted to the target of the pending saccade (Hollingworth, Richard, & Luck, 2008). This attended target then is preferentially processed and consolidated in VSTM, with attention helping to determine what is encoded in this trans-saccadic memory (Hollingworth, Richard, & Luck, 2008; Irwin & Gordon, 1998). While it was the task of VSTM to hold onto the representation of the target in memory across the eye movement, to compare the perceptual information, and if necessary to make corrective saccades (Hollingworth, Richard, & Luck, 2008), attention also continues to linger after the eyes have reached their new landing position (Golomb, Chun, & Mazer, 2008).

During the pre-saccade period visual attention is allocated to the current point of fixation; however, shortly before the saccade is initiated attention is shifted to the future location of fixation (Golomb, Marino, Chun, & Mazer, 2011; Harrison, Mattingley, & Remington, 2012). Spatial attention is held within a retinotopic reference frame that must be updated with each eye movement, while our spatiotopic representation of space remains stable (Golomb, Marino, Chun, & Mazer, 2011). Using a novel gaze-contingent behavioral paradigm, studies employing visual probes at various times during a saccade investigated the mapping of spatial attention (Golomb, Marino, Chun, & Mazer, 2011). Even when the demands of the task were set up to emphasize a spatiotopic reference frame and the retinotopic location was no longer behaviorally relevant, there was always evidence for spatial attention lingering in retinotopic coordinates up to 200ms after the eye movement, with spatiotopic representations taking over at later delays (Golomb, Marino, Chun, & Mazer, 2011). However, in a task where a retinotopic reference frame was emphasized there was limited evidence for spatial attention at spatiotopic coordinates (Golomb, Marino, Chun, & Mazer, 2011).

This pattern of results suggests that spatial attention is maintained in retinotopic coordinates, with updating to spatiotopic coordinates occurring over time and only when it is behaviorally necessary to do so (Golomb, Marino, Chun, & Mazer, 2011). The researchers further argued that when attention is maintained across a saccade then attention only needs to be updated when the representations must be maintained in spatiotopic coordinates (Golomb, Marino, Chun, & Mazer, 2011). Within a spatiotopic reference frame, a new population of neurons must become active with the previous population tapering off after the eye movement, while the facilitation seen in retinotopic coordinates would not need to shift (Golomb, Marino, Chun, & Mazer, 2011).

Retinotopic attentional trace

There has been further investigation into this lingering attentional facilitation at retinotopic locations that lasts up to around 100ms after the saccade, termed the retinotopic attentional trace (Golomb, Pulido, Albrecht, Chun & Mazer, 2010; Golomb, Marino, Chun, & Mazer, 2011; Jonikaitis, Szinte, Rolfs, & Cavanagh, 2013). The literature on the retinotopic attentional trace hints at the slower dynamics of remapping of attention across saccades. The robust nature of the retinotopic attentional trace has been demonstrated in tasks requiring actively sustained attention, regardless of salient spatiotopic cues such as a background grid presented behind the stimuli, where attention continues to linger in retinotopic coordinates (Golomb, Pulido, Albrecht, Chun & Mazer, 2010). These representations were only updated to spatiotopic coordinates when it became behaviorally necessary (Golomb, Pulido, Albrecht, Chun & Mazer, 2010).

In particular, studies with fMRI and ERPs provide complimentary evidence that attentional facilitation persists at previous retinotopic locations when attention shifts to a new retinotopic location following a saccade (Golomb, Nguyen-Phuc, Mazer, McCarthy, & Chun, 2010). fMRI showed blood oxygen level-dependent (BOLD) response activity consistent with retinotopic facilitation in V4 following the saccade, even when behavior was biased toward holding representations in spatiotopic coordinates, with a slow shift to spatiotopic representations over the time course of several seconds (Golomb, Nguyen-Phuc, Mazer, McCarthy, & Chun, 2010). The superior temporal resolution of ERPs provides supporting evidence that the retinotopic attentional trace is maximal 50-100ms following the saccade (Golomb, Nguyen-Phuc, Mazer, McCarthy, & Chun, 2010). The retinotopic attentional trace shows attentional modulation of the anterior N1 component and seems to be strongest for sustained spatial working memory that rehearsed spatiotopic locations (Golomb, Nguyen-Phuc, Mazer, McCarthy, & Chun, 2010).

Tasks with behaviorally irrelevant probes looking at visual elicited ERPs have shown enhanced P1 components between 80 and 100ms at occipital and medial parietal sites following contralaterally presented probes at the retinotopic location (Talsma, White, Mathôt, Munoz, & Theeuwes, 2013). In contrast, a reduced P1 component was found when the probe was presented at the spatiotopic location (Talsma, White, Mathôt, Munoz, & Theeuwes, 2013). Although these results differ slightly from those found in previous papers (Golomb, Nguyen-Phuc, Mazer, McCarthy, & Chun, 2010), the results provide complimentary evidence for the retinotopic attentional trace and the employment of a retinotopic reference frame for eye movements and the differences in the locations and components of interest was likely due to the particular task requirements used (Talsma, White, Mathôt, Munoz, & Theeuwes, 2013).

ATTENTION ACROSS SACCADES

With attention shifting to the target of the saccade and lingering at the previous point of fixation, is there a region of facilitation between the two fixation points? Following the spotlight metaphor, one might assume that for a single locus of attention to sweep between two points of space it must at some point highlight the intermediate space between the two resting points. However, studies probing intermediate locations between the starting and ending points of saccades showed no evidence for attentional facilitation sliding continuously between the two points following the eye movement (Golomb, Marino, Chun, & Mazer, 2011). Instead they found evidence for lingering facilitation at the previous retinotopic location that slowly decays over time, while a secondary representation builds at the new spatiotopic location (Golomb, Marino, Chun, & Mazer, 2011).

However, investigating for such continuous shifts of visual attention before an eye movement has revealed some attentional facilitation at intermediate locations along the trajectory between the retinotopic and future-field locations (Harrison, Mattingley, & Remington, 2012). Probes presented in the intermediate locations showed significant cueing effects, revealed as benefits in response times (Harrison, Mattingley, & Remington, 2012). Importantly, this region of attentional facilitation was in the direction of the upcoming saccade, rather than translationally shifted equidistant but in the opposite direction that would be suggested by shifts in neural receptive fields (Harrison, Mattingley, & Remington, 2012). The results, therefore, suggest more about how attention is allocated during the pre-saccade period (Harrison, Mattingley, & Remington, 2012). These results are not directly comparable to those of Golomb, Marino, Chun, & Mazer (2011) as locations investigated in the studies were within different reference frames. While Golomb and colleagues (2011) defined the locations based on the spatiotopic locations before the saccade, which would place them in the opposite direction as the eye movement, Harrison, Mattingley, & Remington (2012) selected their probed locations in the same direction as the eye movement.

Further behavioral research showed that when a task irrelevant color cue was flashed before an eye movement, attention shifted to the future retinotopic location of the cue although the eyes have not yet begun to move (Jonikaitis, Szinte, Rolfs, & Cavanagh, 2013). Attention was sustained at the location in spatiotopic coordinates, regardless of the changes in retinotopic coordinates, with attentional facilitation decaying quickly at the retinotopic location after the eye movement was completed (Jonikaitis, Szinte, Rolfs, & Cavanagh, 2013). The allocation of attention must have occurred predictively because the removal of the cue during the saccade itself had no effect (Jonikaitis, Szinte, Rolfs, & Cavanagh, 2013).

Pre-saccadic shifts of attention then have further consequences on vision that can help the observer search through a visual environment (Zhao, Gersch, Schnitzer, Dosher, & Kowler, 2012). In this way, attention can act to scout out the next visual environment before the eyes land during a string of saccades. When performing a perceptual search task, performance was better at eventual goals of saccades than at other locations regardless of memory load, contrasts of the stimulus, and presence of superimposed visual noise (Zhao, Gersch, Schnitzer, Dosher, & Kowler, 2012; Kowler, Anderson, Dosher, & Blaser, 1995). These findings suggest that these shifts of attention that occur before eye movements help to modulate the quality of the visual representations, perhaps acting on the relative levels of signal to noise, as seen with enhanced neural responses at target locations (Zhao, Gersch, Schnitzer, Dosher, & Kowler, 2012). Directly testing the impact of a pending eye movement on enhancement of neural activity related to behavioral performance, microstimulation in FEF in monkeys showed improved performance only for the attended item within the range of the stimulated area of cortex, during a spatial attention task at sub-threshold for initiating the saccade (Moore & Fallah, 2001).

Related to the premotor theory of spatial attention, there is growing evidence that oculomotor planning and covert shifts of visuospatial attention may use overlapping cortical areas (Casarotti, Lisi, Umiltà, & Zorzi, 2012). Attentional allocation itself can also be defined at the neuronal level when the collective activity of certain neurons comes to represent one location instead of another (Schall, 2004b). Neurons in FEF have been implicated in covert and overt shifts of attention as well as in various stages of pro-, anti-, and no saccade singleton search tasks (Schall, 2004b). Studies showed that activity in FEF could be related to guiding attention even in the absence of saccades, though it is most commonly associated with saccade production (Schall, 2004b). Single-unit recordings have also shown that attentional selection, for example of singleton targets, and selection of the endpoint of a saccade appear to be supported by separable types of neurons in FEF, which suggests that selection of these two types of targets are distinct processes (Sato & Schall, 2003). Some of the overlapping cortical areas in visual attention and saccades can also show differential contributions to one process over the other (Powell & Goldberg, 2000).

Perceptual/visual stability

Now that we have all the puzzle pieces for eye movements, attention, and visual working memory, it is time to put them together to investigate how we maintain a stable visual world despite all of the challenges and complications mentioned above. There is a rich history of theories in the field of perceptual and visual stability that has tried to understand how disparate snapshots can be turned into conscious perception of a continuous visual world. Any plausible theory must take into account why we do not experience movement despite our eyes moving around three times every second, as well as how differences in visual input before and after an eye movement are reconciled. It is also important to note that stability is most likely not for our entire visual world, but instead for the select items that we are able to attend to across the eye movement. Finally, theories must be able to explain the systematic errors that can be observed in the peri-saccadic time period such as mislocalization of objects briefly presented around the time of saccades while objects that remain visible are not vulnerable to spatial instability despite much larger trans-saccadic displacements (Cicchini, Binda, Burr, & Morrone, 2013; McConkie & Currie, 1996).

Proposed solutions have included: elimination, whereby the efference copy subtracts out the effect of the eye movement, translation, which would rely on an as of yet undiscovered overall spatiotopic map, and evaluation, where a stable map is held in mind and changes are only made when updating is required (Bridgeman, Van der Heijden, & Velichkovsky, 1994). More recent theories build off of this third type of mechanism, where the world is assumed to be stable unless there are salient changes, particularly those that fall within the focus of attention (Mathôt & Theeuwes, 2011). The pre-saccadic shifts of attention could come into play by helping to find any blatant differences between pre- and post-saccade images before the eyes land (Mathôt & Theeuwes, 2011). Then, representations of attended items can somehow be 'remapped' to stay consistent with their new retinotopic location following the eye movement (Mathôt & Theeuwes, 2011).

Neural evidence related to perceptual/visual stability

Much of the recent literature on visual stability takes neural evidence into consideration, and thus tries to explain behavioral observations that have detectable neural correlates. Deficits seen in patients with PPC lesions and single-unit recordings in LIP in primates informed research using TMS over PPC to see if disruption of that area of cortex can impact visual stability (Chang & Ro, 2007). The study did find effects on sensitivity to detecting displacement of stimuli following an eye movement, particularly when TMS was applied to the contralateral hemisphere (Chang & Ro, 2007). Parietal cortex and frontal cortex continue to be areas of interest in visual stability as they receive anticipatory information before the eye movement and are related to the corollary discharge pathway that carries information about the eye movement itself (Wurtz, Joiner, & Berman, 2011; Wurtz, 2008).

Targeting right human frontal cortex with continuous theta-burst stimulation (cTBS) systematically impacted trans-saccadic perceptions of displacement (Ostendorf, Kilias, & Ploner, 2012). This disruption of visual space across eye movements may have been due to reduced internal estimates of the amplitude of the saccade that was made (Ostendorf, Kilias, & Ploner, 2012). Frontal cortex monitors oculomotor actions to help integrate our perception of space across eye movements and likely contributes one of the variables for the visual stability calculation (Ostendorf, Kilias, & Ploner, 2012).

More recent theories have abandoned explicit spatiotopic maps of the world as a way to organize trans-saccadic representations, while proposing other mechanisms such as remapping of attentional pointers to explain perceptual stability (Cavanagh, Hunt, Afraz, & Rolfs, 2010). With this system it would be possible to transfer neural activation for attended items in anticipation of the saccade without having to shift the receptive fields of the neurons themselves (Cavanagh, Hunt, Afraz, & Rolfs, 2010). This would also preclude the transfer of feature detectors that would ordinarily adapt to constant stimulation over time (Cavanagh, Hunt, Afraz, & Rolfs, 2010). However, the authors did concede to other neural evidence of more straightforward trans-saccadic remapping.

REMAPPING

Many of these theories of perceptual stability mention a remapping mechanism that updates where mental representations of visual stimuli are located to match current visual inputs following an eye movement. One classic study that made up much of our early understanding of remapping focused on translational shifts of receptive fields. A single-unit recording study trained monkeys to fixate a certain point while they recorded from a neuron with a receptive field sensitive to a certain area in the visual field (Duhamel, Colby, & Goldberg, 1992). When a stimulus was then presented in this area this first neuron's firing rate increased, while the activity for a second neuron whose receptive field was for a different area did not fire. However, when the monkey then made a saccade to a lateral fixation point that brought the stimulus into the receptive field of the second neuron there was evidence for remapping (Duhamel, Colby, & Goldberg, 1992). The second neuron's activity ramped up even before the saccade was initiated (prospective remapping), while the activity for the first neuron ramped down (truncation) (Duhamel, Colby, & Goldberg, 1992). The authors concluded that this abrupt shift of activity, where neurons hand off their task of firing to another neuron that will have its receptive field brought over a stimulus of interest even before the saccade was initiated, could play a key role in perceptual stability, as we plan an eye movement neurons will start to encode for the new area of visual space (Duhamel, Colby, & Goldberg, 1992). However, this quick exchange is surprising if, in fact, remapping takes place before the eyes start moving, then this would suggest that we would need to remap space with every eye movement.

Working from the knowledge that parietal cortex operates in multiple reference frames, research has employed a double-step task where two future fixation locations are flashed on the screen while the monkey is fixating to test how excitation is shifted across reference frames with an eye movement (Colby & Goldberg, 1999). The monkey must move its eyes to the first fixation point, which would be within the reference frame in which it was originally encoded; however, it must then move its eyes to the second fixation point, which from this new location would require additional calculations to adjust the motor plan to accurately perform the task (Colby & Goldberg, 1999). The findings were very similar to those of Duhamel, Colby, & Goldberg (1992) with gradual remapping occurring in the peri-saccadic period (Colby, & Goldberg, 1999). Further research in single unit recordings found fewer responsive cells and at later durations following saccade initiation in extrastriate visual areas (Nakamura & Colby, 2002) as well as responses at differing time courses in LIP (Kusunoki & Goldberg, 2003).

Predictive remapping

One of the hallmarks of the remapping literature is that the updating between pre- and post-saccadic representations at least starts to take place before the saccade is initiated, which is referred to as predictive remapping (Mathôt & Theeuwes, 2010a). Importantly, predictive remapping of receptive field responsitivity within retinotopic space is related to changes in the locus of attention before the eye movement as well (Mathôt & Theeuwes, 2010a). These changes in attentional facilitation can be seen as greater perceptual accuracy (Hall & Colby, 2011) at the retinotopic location of the attended items following the saccade, not just the saccade endpoint itself (Mathôt & Theeuwes, 2010a; Rolfs, Jonikaitis, Deubel, & Cavanagh, 2011; Jonikaitis, Szinte, Rolfs, & Cavanagh, 2013).

Electrophysiological evidence for predictive remapping of visual processing in humans has been found in ERPs time-locked to the onset of the saccade (Parks & Corballis, 2008; Petersburs, Gajda, Hoffmann, Daum, & Bellebaum, 2011). Participants were presented with a salient grating in-between central fixation and a laterally presented point that they would eventually need to saccade to, or outside of this saccade trajectory (Parks & Corballis, 2008). When the saccade was made over the grating, and thus switched which visual hemifield the grating was presented in, there was evidence for increased pre-saccadic potentials in both hemispheres, with the ipsilateral hemisphere anticipating the stimulation coming into its territory following the eye movement (Parks & Corballis, 2008). A replication and extension by the same group examining the pre-saccadic period showed ipsilateral positivity when the saccade needed to cross the visual grating, and contralateral positivity when the grating was outside the saccade trajectory (Parks & Corballis, 2010). Examining the post-saccadic period showed a similar pattern of results providing evidence for their claim that the activity reflected predictive remapping of space in anticipation of the upcoming saccade (Parks & Corballis, 2010).

Remapping in other contexts

Although some research has attempted to suggest alternative functions for spatial remapping (Bays & Husain, 2008), most of the literature has kept some ties to the original foundation in visual stability although applying the concept of remapping to other areas. One study looked at the impacts on the magnitude of the tilt aftereffect depending on attention or saccadic eye movements (Melcher, 2009). Selective attention and remapping across saccades both reduced the tilt aftereffect, although since the effects were additive the author suggested different underlying mechanisms (Melcher, 2009). The effect of saccadic remapping was potentially due to incomplete transfer of adaptation to the new retinotopic location (Melcher, 2009).

Another study exploited the underlying mechanisms of spatial remapping across saccades by asking participants to remember the location of a flashed cue in an fMRI task (Medendorp, Goltz, & Vilis, 2005). The participant then started to plan a saccade, either toward the remembered location or away from it, performing an anti-saccade (Medendorp, Goltz, & Vilis, 2005). Initial activity was contralateral to the side where the target had been presented; however, if the saccade cue indicated to perform an anti-saccade, away from the side of the remembered location, activity shifted to the ipsilateral hemisphere (Medendorp, Goltz, & Vilis, 2005). The authors argued this was evidence for PPC representing the target location of the saccade, rather than the location of the remembered location, within the context of an anti-saccade task (Medendorp, Goltz, & Vilis, 2005; Medendorp, Goltz, Vilis, & Crawford, 2003).

Remapping across hemispheres

Neuroimaging and electrophysiology in humans has also provided evidence for different insights into remapping following the saccade. During an fMRI task a stimulus was flashed in the center of the screen while participants fixated laterally and then, once the stimulus was extinguished, made a saccade over the location where the stimulus had appeared so that the stimulus' location was brought into the opposite visual hemifield (Merriam, Genovese, & Colby, 2003). The response to the stimulus appeared in the contralateral hemisphere; however, following the eye movement a remapped response of smaller amplitude appeared in the ipsilateral hemisphere after a delay (Merriam, Genovese, & Colby, 2003). This would be consistent with remapping where ipsilateral activity slowly built over time but with less amplitude than the visual response (Merriam, Genovese, & Colby, 2003). Their results were clarified with a follow up study showing that the activity they identified as remapping could not just be attributed to visual or oculomotor responses (Merriam, Genovese, & Colby, 2007).

Research has looked into hemispheric asymmetries in remapping as well as where in the visual stream it is likely to take place. As revealed with patient studies, the transfer of visual information occurring during saccadic remapping likely occurs before parietal cortex in the visual processing stream (Blangero, Khan, Rode, Rossetti, & Pisella, 2011). In other patient work, it appears that the right-hemisphere plays a greater role in transferring information from saccadic remapping to later visual processing areas (Pisella, Alahyane, Blangero, Thery, Blanc, & Pelisson, 2011).

The remapping literature seemed to accept the findings of the classic remapping study (Duhamel, Colby, & Goldberg, 1992); however, recent work has brought to light new evidence that may have far reaching impacts on how we view remapping in the future (Zirnsak, Steinmetz, Noudoost, Xu, & Moore, 2014). In past research it has been shown that visual space is compressed before saccades are initiated, which was seen as tangentially supportive of spatial remapping of receptive fields seen in single-unit recordings (Ross, Morrone, & Burr, 1997). However, in one of the most recent remapping studies, evidence was revealed for receptive fields converging toward the saccade target location rather than shifting a fixed amount equivalent to the retinal displacement following the saccade (Zirnsak, Steinmetz, Noudoost, Xu, & Moore, 2014). The evidence of increased neural firing for certain receptive fields that would fall close to the end point of the saccade is supported; however, this is likely due to the convergence of all receptive fields toward this area during the pre-saccade period (Zirnsak, Steinmetz, Noudoost, Xu, & Moore, 2014). Receptive fields were shown to remap as much as 18 degrees of visual angle, and most importantly even in the opposite direction of the pending saccade if the region originally fell past the saccadic end point (Zirnsak, Steinmetz, Noudoost, Xu, & Moore, 2014).

CONCLUSIONS AND FUTURE DIRECTIONS

When we look at our continuous experience of our visual world it is difficult to imagine all of the challenges, computations, and shifts of attention and gaze that our visual system must deal with every second. From the motor level logistics of creating eye movements, through the many stops in the visual processing stream to track current input and pending eye movements, it is clear that although it adds further complexity, visual working memory and attention are necessary to reciprocally influence all the other stages of processing to generate our conscious perception of a seamless and stable environment. The factors that feed into perceptual stability combine rapid and effective mechanisms for saccade correction and predictive shifts of attention to saccade targets, along with slower processes such as the retinotopic attentional trace and evidence for lingering representations in the original encoding hemisphere during cross-hemispheric remapping. The unique contributions of these processes operating on a range of time courses likely helps explain how our visual system is both able to handle rapid shifts of visual inputs while maintaining a sense of continuity across all of the changes it faces. Although hard remapping of receptive fields in translational shifts directly tied to the amplitude of eye movements was a previous way to help us organize how visual stability might be accomplished, the future of the visual cognition field will now be taking attention further into consideration with recent findings casting new light on previous neural and behavioral evidence.

CHAPTER II

VISUAL WORKING MEMORY REPRESENTATIONS ACROSS EYE MOVEMENTS

INTRODUCTION

Humans make an average of three saccades per second, and each of these eye movements can bring items of interest into new receptive fields and new visual hemifields. As an added layer of complexity, the human visual system is also contralaterally organized, whereby visual information from the left visual hemifield is primarily processed in the right cortical hemisphere, and vice-versa. Researchers continue to investigate the many peri-saccadic phenomena at the intersection between attention and eye movements (Colby, Duhamel, & Goldberg, 1992; Irwin, Zacks, & Brown, 1990; Merriam, Genovese, & Colby, 2003; Hollingworth, Richard, & Luck, 2008; Golomb, Nguyen-Phuc, Mazer, McCarthy, & Chun, 2010). How then do we perceive a continuous world as we look around us? Specifically, how does the brain keep track of where items are in space to help us create this relatively seamless visual experience?

One potential mechanism that could contribute to our conscious perception of a continuous visual experience might be visual working memory (VWM) working to maintain representations of items across saccades. In standard VWM tasks, such as change detection (Luck & Vogel, 1997), where participants are asked to maintain fixation, we see evidence for contralateral representations of items (Vogel & Machizawa, 2004). Electrophysiological activity using ERPs has revealed the contralateral delay activity (CDA), which is a sustained negativity contralateral to the side of the visual field where participants are attending during the delay period between the onset of a memory array and the test (Vogel & Machizawa, 2004). This same activity has also been demonstrated when participants are attending to and monitoring items that remain on the screen (Tsubomi, Fukuda, Watanabe, & Vogel, 2013).

However, how does this work if we are constantly moving our eyes? How do we form a stable representation of items across eye movements? In which hemisphere are the VWM representations predominately represented? Does the representation transfer over to the other side of the brain, constantly shuffling the items between the hemispheres? Or does it stay in the hemisphere contralateral to the visual field where the items were located when we originally created the representation? The consequences of eye movements need to be examined at multiple levels and time points throughout the process. What happens to visual working memory representations when we move our eyes, drawing the items into the other visual hemifield?

Neuroimaging and electrophysiology in humans has provided evidence for remapping following the saccade. A functional magnetic resonance imaging (fMRI) study flashed a stimulus in the center of the screen while participants fixated laterally and then, once the stimulus was extinguished, made a saccade over the location where the stimulus had appeared so that the stimulus' location was brought into the opposite visual hemifield (Merriam, Genovese, & Colby, 2003). The response to the stimulus appeared in the contralateral hemisphere; however, following the eye movement a remapped response of smaller amplitude appeared in the ipsilateral hemisphere after a delay (Merriam, Genovese, & Colby, 2003). ERPs have also revealed that attentional facilitation persists at previous retinotopic locations when attention shifts to a new retinotopic location following a saccade (Golomb, Nguyen-Phuc, Mazer, McCarthy, & Chun, 2010).

In the present experiments we investigated what would happen to working memory representations across saccades in humans using ERPs. What would happen if participants were asked to attend to items in one visual field and then shift their eyes, bringing the items into the other visual field? Based on the saccade literature we would expect to see evidence for remapping, with the representations shifting between hemispheres. Also, we investigated what would happen if participants maintained fixation while being asked to attend to stimuli in one visual field but are then cued to shift their attention to the other visual field, which would have similar visual inputs but may show different types of remapping than changes in eye position. Like the shifting of the N2pc component with shifts of attention during visual search (Woodman & Luck, 1999), the CDA would provide a robust tool to examine the shift of representations between hemispheres.

MATERIALS AND METHODS

Overview

We ran three experiments using a visual working memory task while recording ERPs and eye tracking simultaneously for human participants. Previous research with multiple object tracking (MOT) has shown that the CDA is sensitive to the visual hemifield in which an attended item appears, including maintaining a contralateral representation as the item shifts across visual hemifields (Drew & Vogel, 2008; Drew et al., 2014). Therefore, we expected that shifting attention between visual hemifields should produce a similar effect, with the CDA showing sustained activity contralateral to whichever visual hemifield is currently being attended. We would then use this as a point of comparison for whether the VWM representations also transfer between hemispheres during an eye movement that draws the attended items into the opposite visual hemifield, or if the representations will linger in the original encoding hemisphere.

Participants

We ran 18 participants in Experiment 1, 24 in Experiment 2, and 16 in Experiment 3. All were neurologically normal participants who participated after giving informed consent after the procedures of a protocol approved by the Human Subjects Committee at the University of Oregon. For Experiment 1, 3 participants' data were rejected for corrupted eye tracking files and 1 participant for not following the instructions, resulting in 14 analyzable participants. For Experiment 2, 9 participants' data were rejected for technical issues with the eye tracker and 3 participants who did not complete the tasks, resulting in 12 analyzable participants. For Experiment 3, 3 participants' data were rejected for corrupted eye tracking files and 1 for EEG recording artifacts, resulting in 12 analyzable participants.

Experiment 1

Behavioral procedure

Stimuli were generated using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) for Matlab (MathWorks) on a 17-inch flat cathode ray tube monitor. Using a counterbalanced blocked design, half of the blocks consisted of an attention condition, while the other half employed an eye movement condition. We used a modification of the task introduced in Tsubomi, et al., 2013. In the attention condition, participants fixated a central fixation cross throughout the trial (Figure 1).

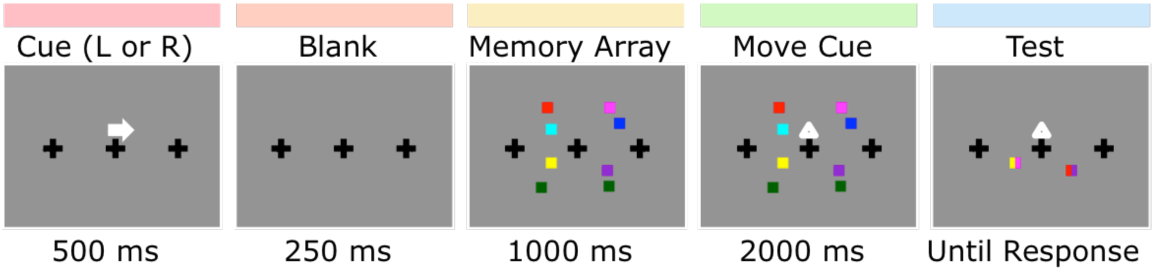

Figure 1. Behavioral procedure for Experiment 1
From left to right, the screens presented to the participant include the Cue indicating which side of the screen to attend to, a Blank display, a Memory Array that remains on the screen until the test, a Move Cue that is presented on the memory array after 1000ms and remains through the test, and a Test.

The central fixation cross appeared with fixation crosses (subtending 0.60 × 0.60° each) laterally displayed to the right and left, separated by 7°. An arrow appeared over the center fixation cross cuing participants to attend to one side (500ms), followed by a blank screen with fixation crosses (250ms). A bilateral memory array of four colored squares (subtending 1.45 × 1.45° each) appeared (no color repeats on same side, from a pool of 9 colors). The squares were horizontally centered between the center and lateral fixation cross (±3.5° from the center of the screen) on each side with an independent random horizontal jitter of ±1.43° and vertical jitter of ±0.53° so that the squares never overlapped. Participants attended to the cued side. The squares remained on the screen until test (1000ms until move cue, 3000ms total). A shape cue appeared over the central fixation cross indicating to either continue attending to squares on the originally cued side, or to switch attention to the squares on the other side with 50/50 chance (2000ms).

All squares then disappeared except for one item on each side, with half of the square being the original color and the other half being a color that did not appear on that side. Participants were asked to indicate which side of the square was the color that was originally at the probed location on the final attended side with a key press (Z or / for left or right respectively). There were 10 blocks of 40 trials each and participants were given accuracy feedback at the end of each block.

In the eye movement condition the stimuli were identical to those used in the attention shifting condition except participants maintained their attention on the original side throughout the trial, and when the cue appeared 1000ms after the onset of the memory array, participants were cued to either maintain central fixation (no move condition) or move their eyes to the lateral fixation cross on the attended side, moving their fixation over the region they are attending. This shifted which visual hemifield the items were presented in. Then, at test, they responded to that originally cued side.

Eye tracking recordings and analysis

Participants were seated at a chinrest set 67cm from the monitor. The position of the participants' eye position was monitored using an Eyelink 1000 (SR Research). The eye tracker was calibrated after every four blocks.

Electrophysiological recordings and analysis

We recorded ERPs using our standard recording procedures (Vogel et al., 1998; McCollough et al., 2007). We recorded from 22 tin electrodes held in place by an elastic cap (Electrocap International) using the International 10/20 system. The 10/20 sites F3, Fz, F4, T3, C3, Cz, C4, T4, P3, Pz, P4, T5, T6, O1, and O2 were used along with five nonstandard sites: OL midway between T5 and O1; OR midway between T6 and O2; PO3 midway between P3 and OL; PO4 midway between P4 and OR; and POz midway between PO3 and PO4. The left-mastoid was used as reference for all recording sites. Electrodes placed ~1cm to the left and right of the external canthi of each eye recorded horizontal electrooculogram (EOG) to measure horizontal eye movements. To detect blinks, vertical EOG was recorded from an electrode placed beneath the left eye and reference to the left mastoid. The EEG and EOG were amplified with an SA Instrumentation amplifier with a bandpass filter of 0.01–80 Hz and were digitized at 250 Hz in LabView 6.1 running on a PC.

We used a modification based on standard analysis procedures, including exclusion of trials containing blinks (Vogel et al., 1998; McCollough et al., 2007). We used the EEGLAB (Delorme & Makeig, 2004) and ERPLAB (Lopez-Calderon & Luck, 2014) toolboxes for EEG and ERP processing, and performed ICA using the Infomax ICA algorithm (Bell & Sejnowski, 1995). Further trial rejections were then made based on the coordinates of the participants' fixations measured by the eye tracking data during windows of interest before (500-800ms after the onset of the memory array) and after the condition cue (2000-2300ms after the onset of the memory array) appeared. Trials where participants' fixations fell outside of a 3.48° radius from the target fixation cross were rejected from further analysis (Figure 2).

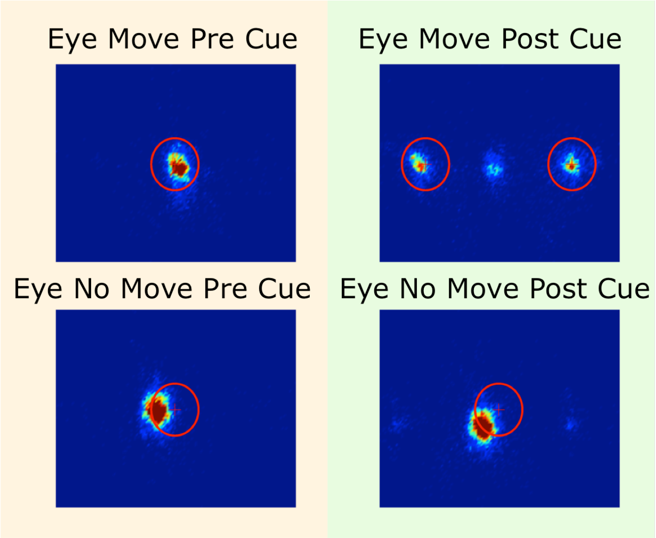

Figure 2. Fixations from Experiment 1
All the participants' fixations as measured by the eye tracker in the eye move and eye no move conditions both pre cue (500 to 800ms from the onset of the memory array) and post cue (2000 to 2300ms from the onset of the memory array). The red circle has a 3.48° radius from the target fixation cross. Any trials where fixations fell outside of this target region during the windows of interest were rejected from further analysis.

Contralateral waveforms were computed by averaging the activity recorded over the right hemisphere when participants attended and remembered items in the array at the left side of screen. Contralateral and ipsilateral will always be described with respect to the original memory array onset for all experiments and conditions. Difference waves were then formed by subtracting the ipsilateral activity from the contralateral activity to examine the CDA at the average of the posterior electrode site pairs PO3/4, O1/2, OL/R, and T5/6.

Experiment 2

The results of the first experiment suggested further examination of the effects of eye movements on VWM representations. In a second experiment we tried to disentangle potential eye movement related activity from the CDA indexing the VWM representations of the items.

Behavioral procedure

In a blocked design, for half of the blocks the stimuli were identical to the eye move condition from Experiment 1 where participants moved their eyes *over* the attended side, switching the visual hemifield where the squares were being presented (Figure 3). In the other half of the blocks the stimuli were exactly the same, except when participants were cued to move their eyes they moved their eyes *away* from the attended side, keeping the attended items in the original visual hemifield, but moving the eyes the same distance in the opposite direction from the Eye Move *Over* condition.

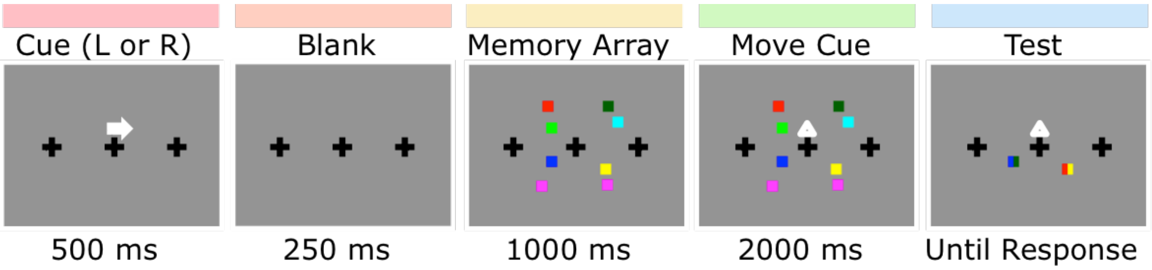

Figure 3. Behavioral procedure for Experiment 2
From left to right, the screens presented to the participant include the Cue indicating which side of the screen to attend to, a Blank display, a Memory Array that remains on the screen until the test, a Move Cue that is presented on the memory array after 1000ms and remains through the test, and a Test.

Therefore, for trials where participants attended each side (left or right) the participants would make an eye movement in a consistent direction with attention (left or right, respectively) or in the opposite direction (right or left, respectively). Therefore, for leftward attention trials where participants were cued to move their eyes, participants would move their eyes to the left on half of the trials and to the right on the other half.

These eye movements would be of equal distance magnitude but in opposite directions which could cancel out potential eye movement related activity when averaged together, thus revealing an underlying CDA to let us more clearly check for signs of remapping.

Eye tracking and electrophysiological recordings and analysis

The same procedures for recording and analysis were used as in Experiment 1.

Experiment 3

In the past experiments with the CDA we have confounded the spatiotopic and retinotopic coordinate systems. Participants have usually fixated the center of the screen whereby the left side was always the left side of the screen as well as the left side of where the participants look. To substantiate our use of the CDA as a tool for examining working memory representations across eye movements we made sure that the CDA is indeed established in retinotopic coordinates.

Behavioral procedure

As with the previous experiments, the displays contained three fixation crosses. The sizes of and distances between the stimuli were the same as in Experiment 1 and 2. Participants were cued to fixate the center of the screen with the central fixation cross turning red at the beginning of each trial (500ms), followed by a blank with the fixation crosses still present (500ms) (Figure 4).

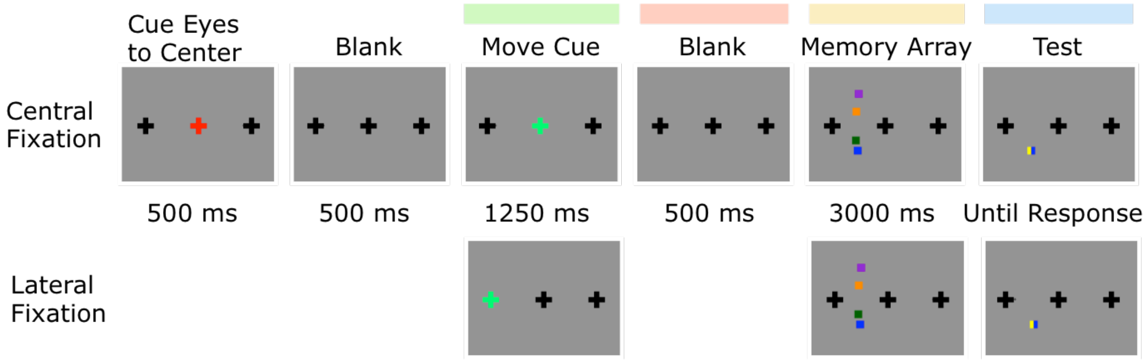

Figure 4. Behavioral procedure for Experiment 3
From left to right, the screens presented to the participant include the Cue instructing to move their eyes back to the center fixation cross for the next trial, a Blank display, a Move Cue that tells participant which fixation cross to look at for this trial, another Blank screen, a Memory Array that remains on the screen until the test, and a Test.

One of the fixation crosses then turned green, either in the center, cueing participants to maintain central fixation, or appeared at one of the lateralized fixation crosses, cueing the participant to move their eyes to a lateral fixation cross (1250ms) followed by a blank with the fixation crosses still present (500ms). A unilateral memory array then appeared that the participants had to attend to (3000ms) up to the test where all of the squares disappeared except for one, as in the previous experiments, where participants had to indicate what color was originally at that location. If the participants were cued to move their eyes to one of the lateral fixation crosses the memory array would then appear on that side of the screen, so that it appeared in the opposite visual hemifield in retinotopic coordinates, but remained on the same side of the screen in spatiotopic coordinates.

Eye tracking and electrophysiological recordings and analysis

The same procedures for recording and analysis were used as in Experiments 1 and 2.

RESULTS

Experiment 1

The first experiment provided controls for both conditions to compare the effects of shifts of attention and eye position on VWM representations, as well as allowing direct comparisons between the attention and eye movement conditions. Critically, Experiment 1 provided a first insight into the contralaterally organized signals related to performing eye movements in relation to the focus of sustained attention.

Behavioral results

Participants performed the working memory task well with mean accuracy around 80.1% (*SD*=8.6%). Trials where the participant did not correctly respond to the working memory test were not included in the final analysis (*M* = 11.64%, *SD* = 7.39%). All percent of trials rejected are with respect to the total number of trials.

Eye tracking results

The average percent of trials rejected for participants fixating outside of target area during the time windows of interest was 20.97% (*SD* = 10.99%) (Figure 2). On average, participants began initiating their saccade at 1702.9ms (*SD* = 70.78ms) after the onset of the memory array, which is 702.9ms after the cue to move their eyes.

Electrophysiology results

Throughout these results, contralateral and ipsilateral activity is always in reference to the side of the screen where participants were attending during the original memory array onset. In the Attend No Move and Eye No Move condition the CDA sustains across the length of the trial in the contralateral-ipsilateral activity difference waves (Figure 5).

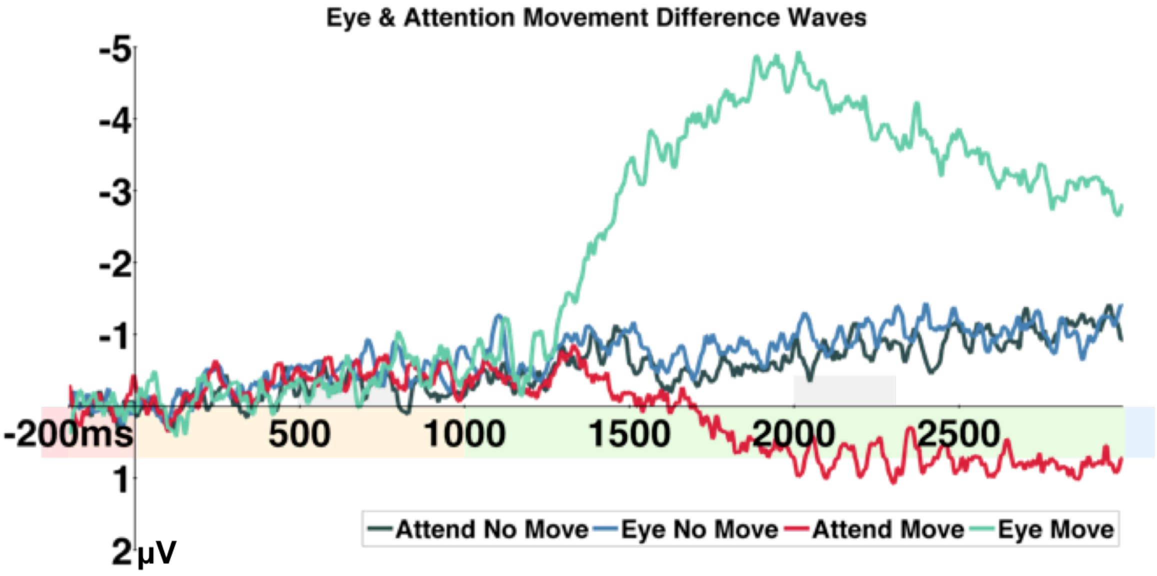

Figure 5. Contralateral – ipsilateral difference waves for Experiment 1 CDA calculated as the difference waves for contralateral – ipsilateral activity at the average of posterior electrode sites. The pre-cue (500-800ms from onset of the memory array) and post-cue (2000-2300ms from the onset of the memory array) that will be used for analyses are highlighted in gray. The move cue appeared at 1000ms from the onset of the memory array, indicated by the change in color from yellow to green on the time axis, consistent with the color code used in Figure 1 and 2 for Experiment 1.

In the attention move condition there is the same initial CDA before the cue followed by an almost instantaneous flip in polarity in the difference waves. Repeated paired samples t-tests with a sliding window of 200ms, overlapping by 100ms, starting at the onset of the cue (1000ms from the onset of the memory array), revealed that CDA for the Attend Move condition (*M* = 0.39, *SD* = 0.94) became significantly less negative than the Attend No Move condition (*M* = -0.495, *SD* = 0.98), indicative of its trajectory into positive polarity, between 1700 and 1900ms, *t*(13) = -2.14, *p* = 0.03. This would be consistent with the participants switching attention to the other visual hemifield and the representation remaining contralateral to the currently attended items. Looking at the contralateral and ipsilateral activity to confirm this, compared to pre-cue contralateral (*M* = -0.31, *SD* = 1.75) and ipsilateral (*M* = 0.14, *SD* = 1.88) activity, following the cue contralateral activity (*M* = -0.28, *SD* = 2.40) decreases while ipsilateral activity (*M* = -1.01, *SD* = 2.23) increases, consistent with dropping the items on the original contralateral side and starting to hold onto the items on the other side (Figure 6).

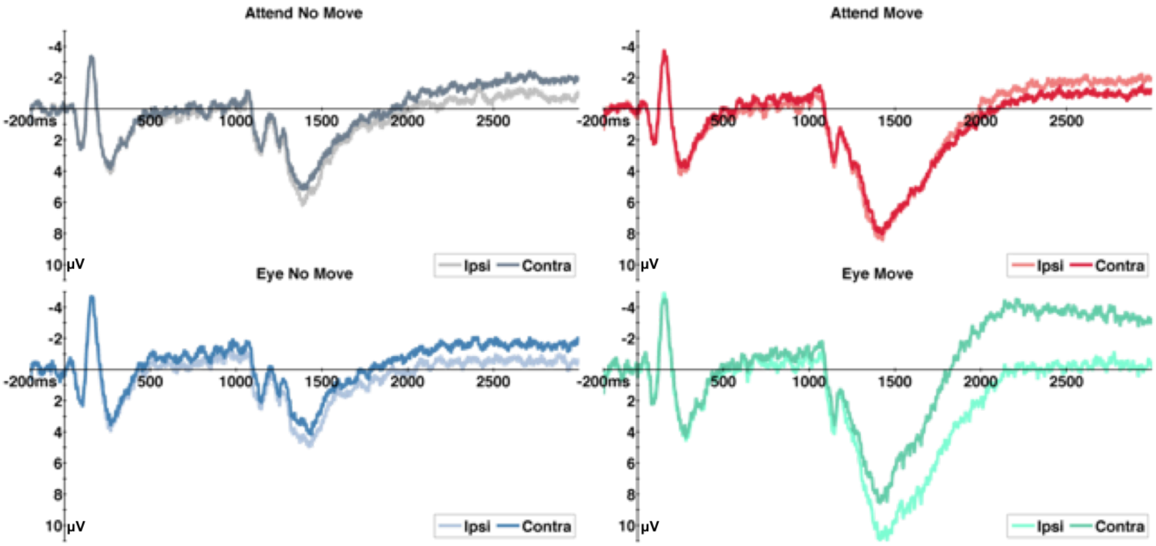

Figure 6. Contralateral and ipsilateral activity for Experiment 1
Contralateral and ipsilateral activity at the average of posterior electrode sites.

To get measurement of when this remapping becomes significant we took a subtraction of the Attend Move condition from the Attend No Move condition so that the initial CDA is set to a baseline of zero (Figure 7). Determined by a more stringent bootstrapping procedure, the remapping of activity, indicative of the shift of attention resulting in a shift of which hemisphere is primarily representing the items, becomes significant at 2098.20ms from the onset of the memory array, and 1098.20ms from the cue to shift attention (p < .01). All of these analyses provide converging evidence that when attention is shifted between visual hemifields the VWM representations are updated to remain contralateral to the currently attended visual hemifield. This is both consistent with our predictions and the MOT literature (Drew et al., 2014). It further validates the CDA as a robust and sensitive component to track VWM representations as they shift between hemispheres.

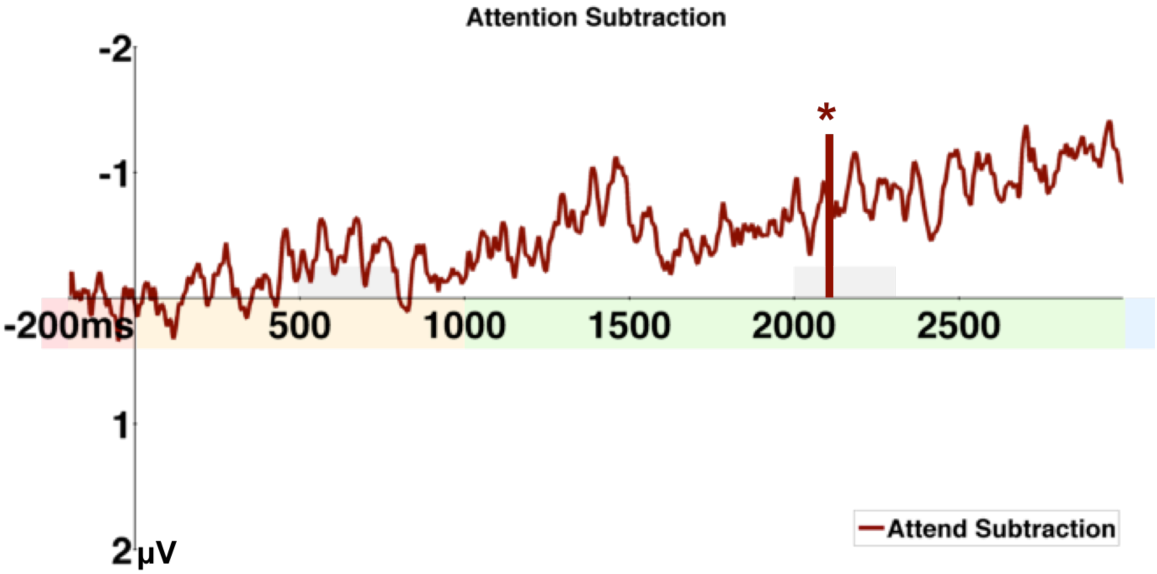

Figure 7. Subtraction of attend no move – attend move for Experiment 1
Subtraction of the contralateral-ipsilateral difference waves for the Attend No Move – Attend Move conditions at the average of the posterior electrode sites. The activity becomes significantly different from the pre cue baseline at 2098.20ms from the onset of the memory array.

We then examined the Eye Move condition. We see the same initial CDA before the cue (*M* = -0.35, *SD* = 0.85); however, following the cue, the contralateral and ipsilateral difference activity (*M* = -4.23, *SD* = 2.30) ramps up, while remaining negative in polarity (Figure 5). Compared to the pre-cue contralateral (*M* = -0.61, *SD* = 2.06) and ipsilateral activity (*M* = -0.26, *SD* = 1.84), following the cue the ipsilateral activity (*M* = 0.48, *SD* = 2.61) decreases slightly, while contralateral activity (*M* = -3.75, *SD* = 2.07) ramps up, consistent with the representation being held in the original contralateral hemisphere where it was encoded (Figure 6). Importantly, looking at the difference wave, the activity does not appear to flip over, becoming positive as seen with the attention move condition. The topography of this contralaterally organized component reveals greater amplitude toward frontal sites (Figure 8).

However, we noted slight decrease in the difference wave activity for the Eye Move condition toward the end of the trial. If we were able to remove the potential eye movement related activity would there be an underlying CDA, and would it show a full flip in polarity, becoming positive, indicative of the item representations remapping to the other hemisphere following the eye movement?

We were confident that the activity seen in the Eye Move condition was not pure bleed over from the horizontal EOG channels (HEOG) as the activity was always negative in polarity, regardless of whether participants were moving their eyes to the left or right. However, considering the topography of the component across electrode sites it was possible that there was some form of eye movement related activity that happened to be contralaterally organized, perhaps associated with the frontal eye fields. Therefore to remove the ramp up we used independent components analysis (ICA) to remove potential HEOG contamination or other eye movement related artifacts.

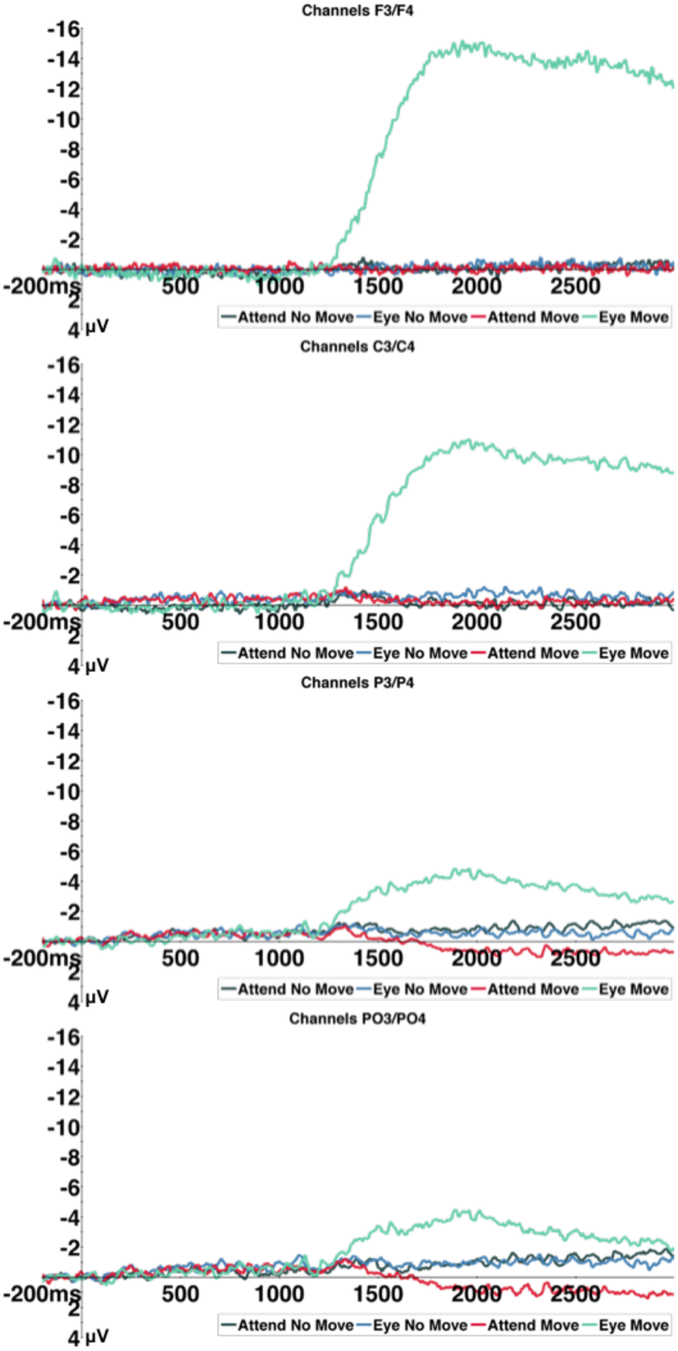

Figure 8. Topography of contralateral-ipsilateral difference waves for Experiment 1 From top to bottom, difference wave activity at electrode sites F3/4, C3/4, P3/4, and PO3/4 depicting greater amplitude activity for the Eye Move condition post cue at the more frontal electrode sites.

For each participant we separated the data by condition and ran ICA on the Eye Move condition separately for left and right. Using all 22 channels we decomposed the data into 22 statistically independent components. For each participant we then removed the component that best captured the horizontal eye movement-related artifacts following the Eye Move cue while showing minimal activation pre cue. The removed components were most localized to the HEOG channel. We then appended each of the conditions together for each participant and created another grand average after the components related to horizontal eye movement artifacts were removed (Figure 9).

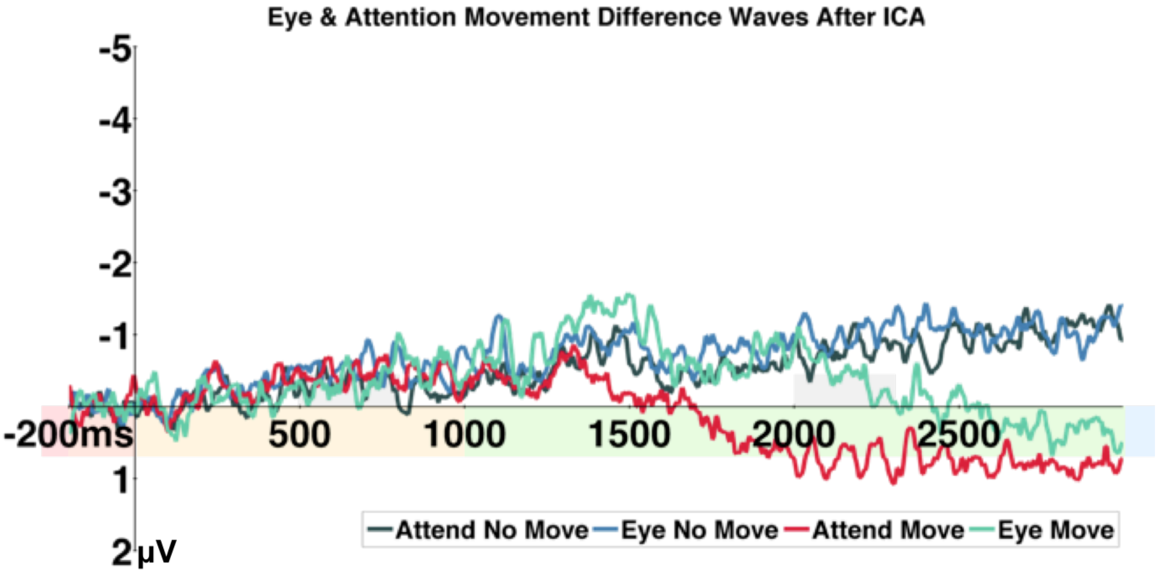

Figure 9. Contralateral – ipsilateral difference waves after ICA for Experiment 1 CDA calculated as the difference waves for contralateral-ipsilateral activity at the average of posterior electrode sites after performing ICA on the Eye Move condition.

As seen in Figure 9 the difference waves for the Eye Move condition dip down to pre-cue levels (M = -0.34, SD = 0.83) following the cue (M = -0.48, SD = 1.24). The ICA procedure seems to have isolated the eye movement related activity and revealed an underlying sustained activity for several hundred milliseconds following the cue before slowly dropping around zero and then positive at the end of the trial.

Experiment 2

The results of the first experiment suggested further examination of the effects of eye movements on VWM representations. In Experiment 2 we will attempt to disentangle potential eye movement related activity from the CDA indexing the VWM representations of the items. We suspected an additive relationship between the CDA and the eye movement related activity and therefore designed Experiment 2 to help experimentally subtract the effects of eye movements. We can also examine the same data using ICA, as in Experiment 1, to examine the underlying activity by parsing out the activity related to the direction of the eye movements themselves. Specifically, in Experiment 2 we wanted to isolate and remove the 'ramp up' in activity that we believed was associated with the eye movement to get a clear look at the underlying CDA to examine what happens to the VWM representation across eye movements.

Behavioral results

Participants performed the working memory task with mean accuracy around 78.19% (SD=6.80%). Trials where the participant did not correctly respond to the working memory test were not included in the final analysis (*M*=8.93%, SD=4.12%).

Eye tracking results

The average percent of trials rejected for participants fixating outside of target area during the time windows of interest was 33.10% (SD=16.85%) (Figure 10). On average, participants began initiating their saccade at 1719.7ms (SD=81.81ms) after the onset of the memory array, which is 719.7ms after the cue to move their eyes.

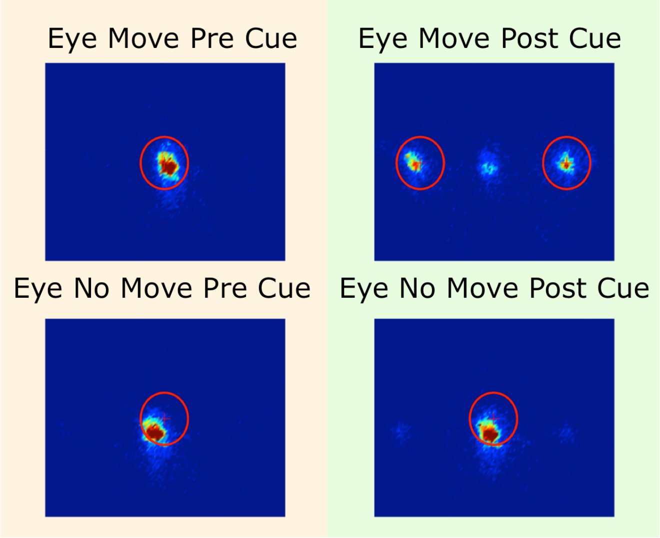

Figure 10. Fixations from Experiment 2
All the participants' fixations as measured by the eye tracker in the Eye Move and Eye No Move conditions both pre cue (500 to 800ms from the onset of the memory array) and post cue (2000 to 2300ms from the onset of the memory array). The red circle has a 3.48° radius from the target fixation cross. Any trials where fixations fell outside of this target region during the windows of interest were rejected from further analysis.

Electrophysiology results

The Eye No Move conditions, intermixed in the Over and Away condition blocks, show a sustained CDA across the length of the trial (Figure 11). The Eye Move Over condition shows the same ramp up in negative activity following the eye movement cue as was seen in Experiment 1, replicating our findings. The Eye Move Away condition shows an equally large deflection in activity, but in positive polarity, opposite of the eye move over condition (Figure 11).

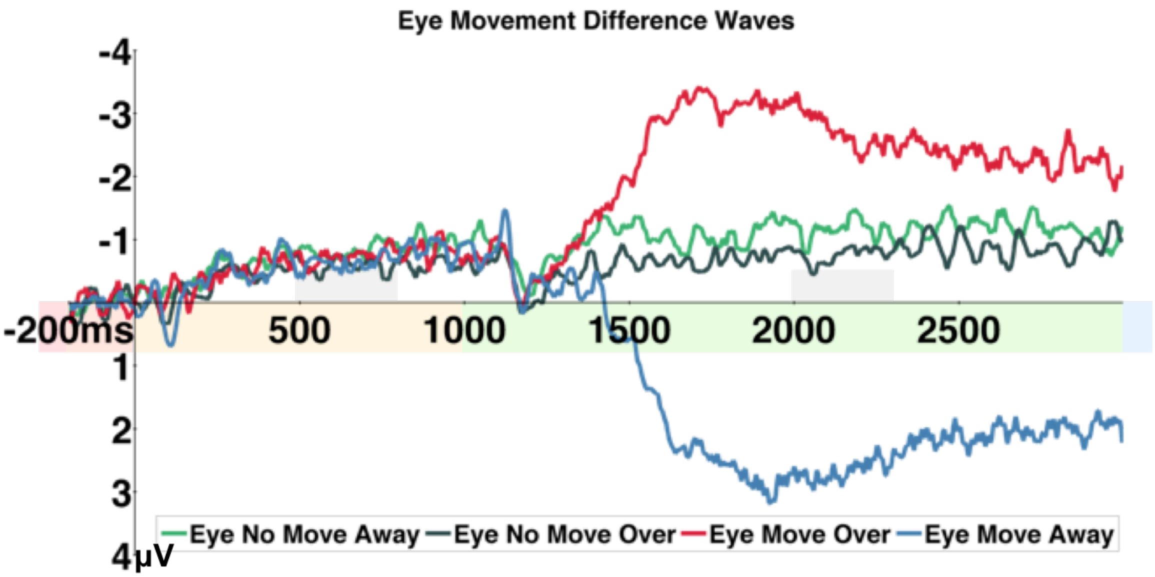

Figure 11. Contralateral – ipsilateral difference waves for Experiment 2
CDA calculated as the difference waves for contralateral – ipsilateral activity at the average of posterior electrode sites.

One might suggest that these deflections in activity could be contamination from the HEOG, as the HEOG is characterized by deflections in opposite polarity for eye movements to the left or right. However, by examining activity with respect to contralateral and ipsilateral recording sites we are collapsing across rightward and leftward eye movement trials, with the HEOG, necessarily cancelling out to zero. To further illustrate that the HEOG is sensitive purely to the direction of the eye movement, regardless of which visual hemifield is being attended, we plotted the HEOG with respect to which side of the screen is being attended in the trial (left or right attention trials for Eye Move Over and Eye Move Away conditions) (Figure 12). While the deflections in the difference waves (Figure 11) are sensitive to *where the items are being attended*, the HEOG activity is based only on the *direction of eye movement* (for example, rightward eye movements show negative polarity for right attend Eye Move Over trials and left attend Eye Move Away trials).

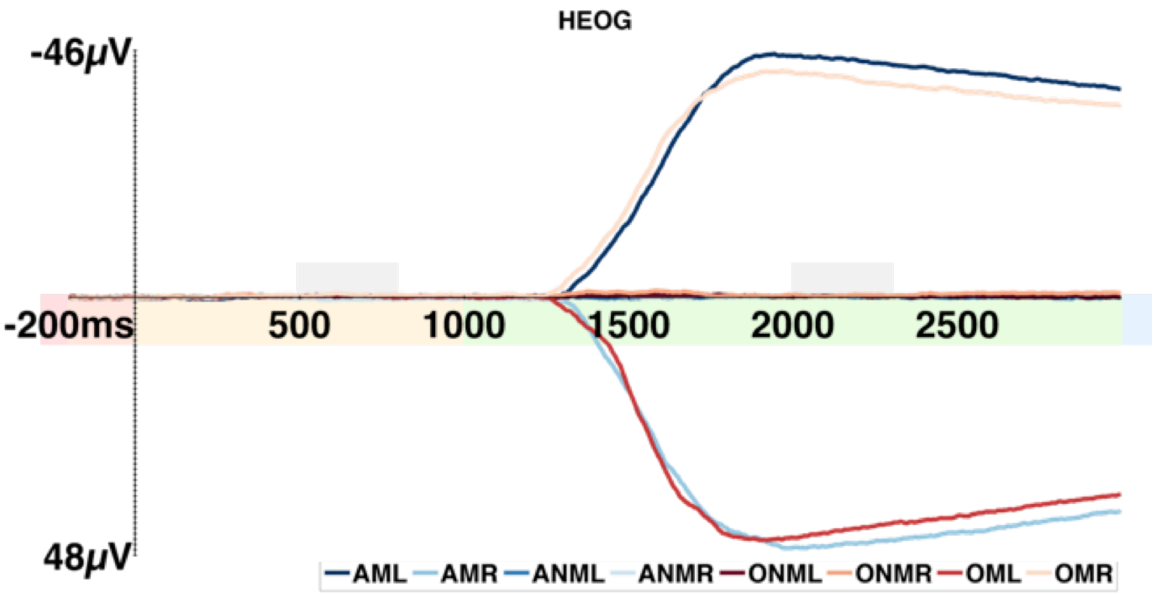

Figure 12. HEOG activity for Experiment 2
Legend labels indicate A (Away) or O (Over), NM (No Move) or M (Move), and L (Left) or R (Right) where the side indicates the direction of attention. Importantly, the Eye Move Away condition where participants are attending to the left (AML) has the participants moving their eyes to the right which is depicted as a large deflection in negative polarity and matches the activity seen in the Eye Move Over condition when participants are attending to the right (OMR). The same pattern can be seen in positive polarity for AMR and OML. Therefore, polarity of HEOG activity is determined by the direction of the eye movement, irrespective of the direction of attention.

Considering this finding, we attempted to rule out HEOG contamination as a potential explanation for the deflections in the difference wave activity by averaging together the Eye Move Over and Away conditions. For the average of the Eye No Move conditions ((Eye No Move Over + Eye No Move Away)/2) there is a sustained CDA to which we can compare the average of the Eye Move conditions ((Eye Move Over + Eye Move Away)/2) (Figure 13). Averaging the negative deflection of the Eye Move Over and positive deflection of the Eye Move Away conditions reveals the underlying CDA. Does the activity flip over, becoming positive like the attention move condition, which would be indicative of the VWM representations shifting between hemispheres? We see the same initial CDA before the cue (*M* = -0.68, *SD* = 0.57) and then activity holds for several hundred milliseconds following the cue before eventually reaching zero (*M* = -0.02, *SD* = 0.52) (Figure 13). Although the activity decreases toward the end of the trial it does not flip in polarity to become fully positive.

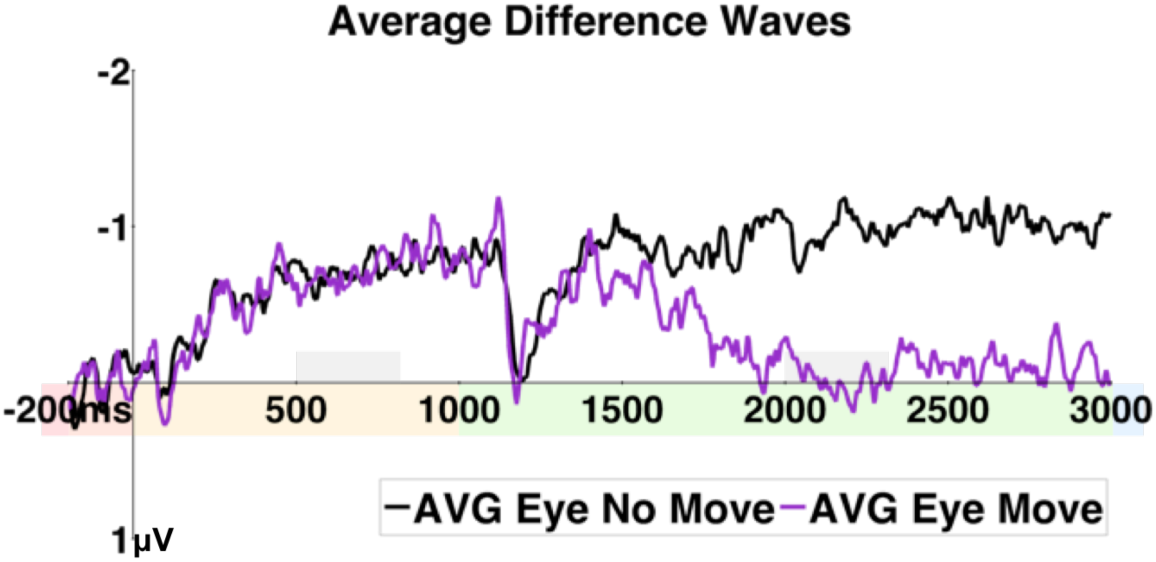

Figure 13. Average of difference waves for eye no move and move for Experiment 2 Average of the contralateral-ipsilateral difference waves at the average of the posterior electrode sites for the Eye No Move and Eye Move conditions. Averaging together the Eye Move Away and Eye Move Over condition removes the contralateral eye movement activity revealing the underlying VWM representation as indexed by the CDA.

To examine why this is the case, we looked at the contralateral and ipsilateral activity for the averaged Eye Move Over and Eye Move Away conditions and see that the contralateral activity remains at the same level following the cue (*M* = -1.24, *SD* = 2.18) as before the cue (*M* = -0.74, *SD* = 1.13), rising only slightly, whereas ipsilateral activity increases (*M* = -1.23, *SD* = 2.25) compared to pre-cue (*M* = -0.06, *SD* = 1.08), becoming more negative, rising up to meet the contralateral activity (Figure 14). Repeated paired samples t-tests with a sliding window of 200ms, overlapping by 100ms, starting at the onset of the cue (1000ms from the onset of the memory array), revealed that contralateral activity for the average of the Eye Move conditions (M = -0.73, SD = 2.11) was no longer significantly different from the ipsilateral activity (M = -0.611, SD = 2.27), between 1900 and 2100ms from the onset of the memory array or between 900 and 1100ms after the move cue, $t(11) = -0.87$, $p = 0.20$. This is consistent with the representation holding in the hemisphere contralateral to the original memory onset throughout the length of the trial, while a representation is slowly formed in the ipsilateral hemisphere several hundred milliseconds following the eye movement.

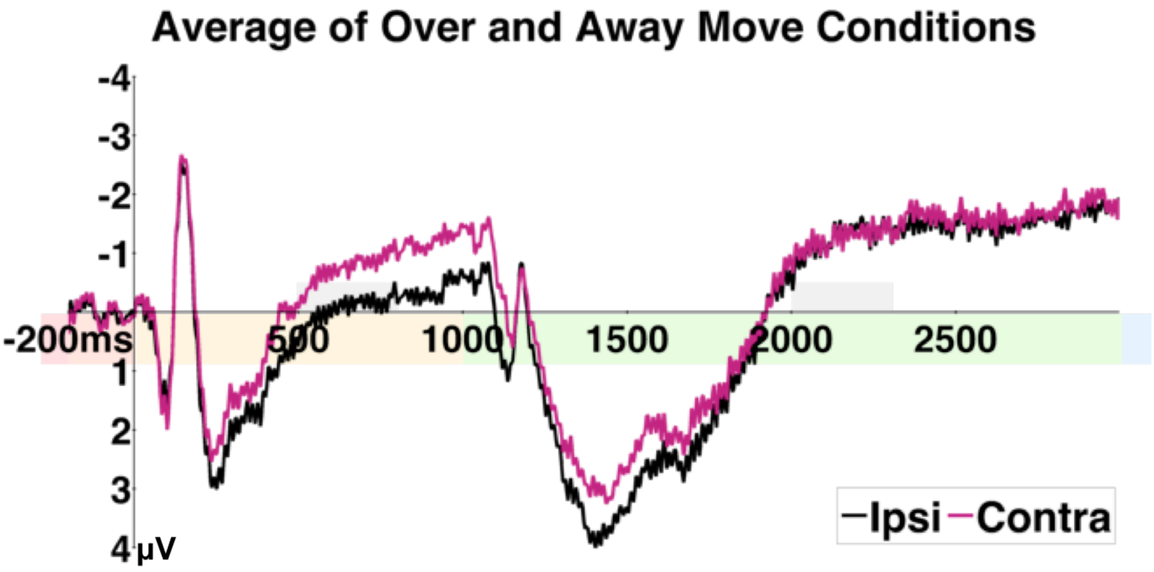

Figure 14. Contralateral and ipsilateral activity for average eye move for Experiment 2 Contralateral and ipsilateral activity at the average of the posterior electrode sites for the average of the Eye Move Away and Eye Move Over conditions.

After collapsing out the eye movement related activity, we then performed the same subtraction as for the attention condition in Experiment 1. Using the average of the Eye No Move conditions' CDA as the baseline we can examine any shifts of VWM representations activity between hemispheres (Average Eye No Move – Average Eye Move) (Figure 15).

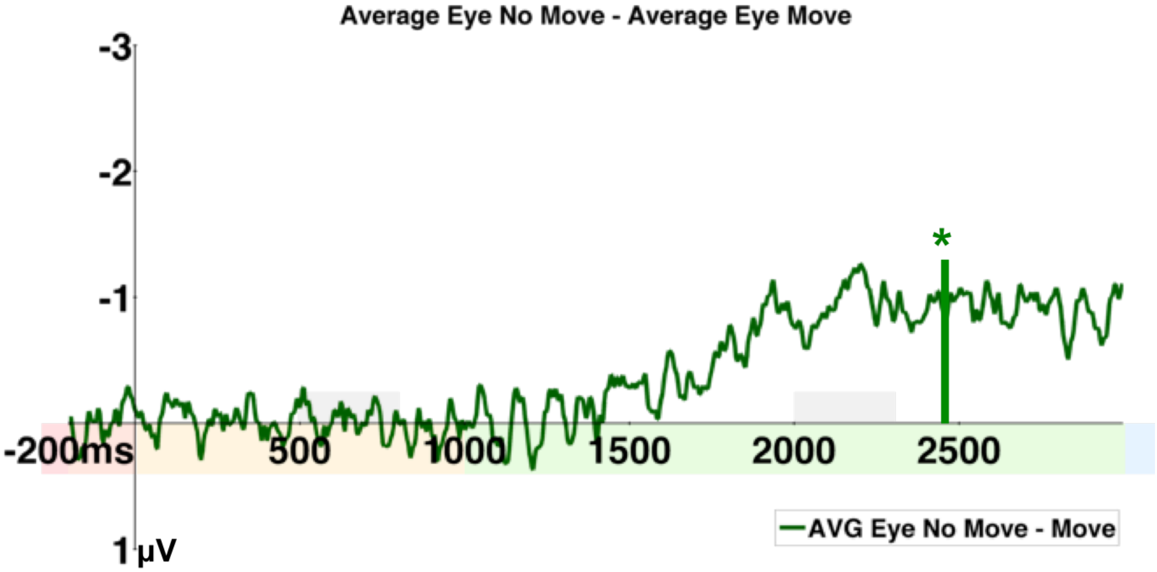

Figure 15. Subtraction of average eye no move – average eye move for Experiment 2 Subtraction of the contralateral-ipsilateral difference waves for the average Eye No Move - average Eye Move conditions at the average of the posterior electrode sites. The activity becomes significantly different from the pre cue baseline at 2459.20ms from the onset of the memory array.

The amplitude of the eye movement (*M* = -0.94, *SD* = 1.30), subtraction is less than that seen in the attention subtraction (*M* = -1.52, *SD* = 1.33) in Experiment 1 following the cue. Using the same bootstrapping procedure, the eye movement subtraction significantly deviates from the baseline 2459.20ms from the onset of the memory array, and 1459.20ms from the cue to move the eyes (p < .01). This is almost half a second after the attention condition showed significant deviation from baseline in Experiment 1. As these measurements are between samples, rather than within, we are cautious to come to any conclusions. However, this would be consistent with the dynamics seen in the contralateral and ipsilateral activity. When looking to the contralateral and ipsilateral activity the contralateral activity remains at the same level, consistent with the representation being held in the hemisphere contralateral to the original memory array onset. However, over time, around one full second following the move cue, the ipsilateral activity builds to reach the same level of activity, consistent with a representation building in the new hemisphere by the end of the trial. This appears to be evidence for an eventual building of a VWM representation in the ipsilateral hemisphere following an eye movement, but not a full shift of VWM representation from the contralateral to ipsilateral hemisphere as was seen in the Attend Move condition in Experiment 1.

We also used ICA as a second method to remove potential HEOG contamination. We used the same procedures as in Experiment 1 to remove the components potentially related to horizontal eye movement artifacts. ICA was completed on each of the conditions separately, without averaging the Eye Move Over and Eye Move Away conditions. The contralateral and ipsilateral difference waves show that the positive and negative deflections have been removed (Figure 16).

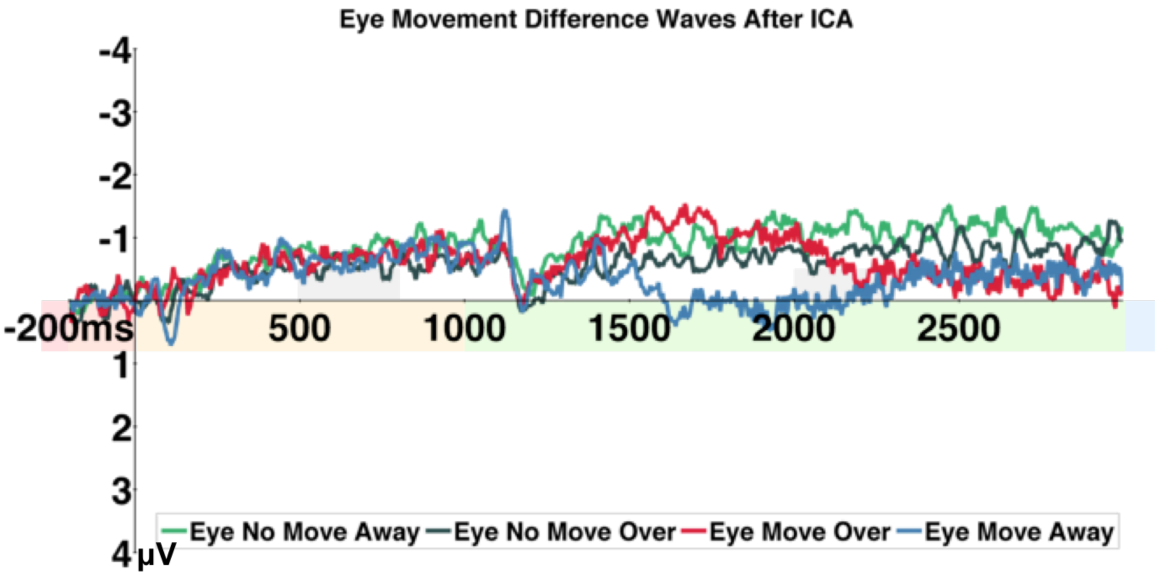

Figure 16. Contralateral – ipsilateral difference waves after ICA for Experiment 2 CDA calculated as the difference waves for contralateral-ipsilateral activity at the average of posterior electrode sites after performing ICA on the Eye Move Over and Away conditions.

The contralateral and ipsilateral activity for the Eye Move Over condition shows a similar pattern of activity that we saw through the averaging method. The difference (*M* = -0.70, *SD* = 0.62) between the pre-cue contralateral activity (*M* = -0.62, *SD* = 1.20) and ipsilateral activity (*M* = 0.07, *SD* = 1.06) decreases following the cue at the very end of the trial between 2800 and 3000ms from the onset of the memory array (*M* = -0.35, *SD* = 0.76) between the contralateral (*M* = -0.54, *SD* = 1.81) and ipsilateral (*M* = 0.07, *SD* = 1.28) activity (Figure 17). The decrease trends toward significance, *t*(11) = 1.38, *p* = 0.098), where importantly, the difference is still negative. It does not switch over to become positive. This is consistent with the VWM representation remaining in the contralateral hemisphere with indications of an eventual sharing across the hemispheres.

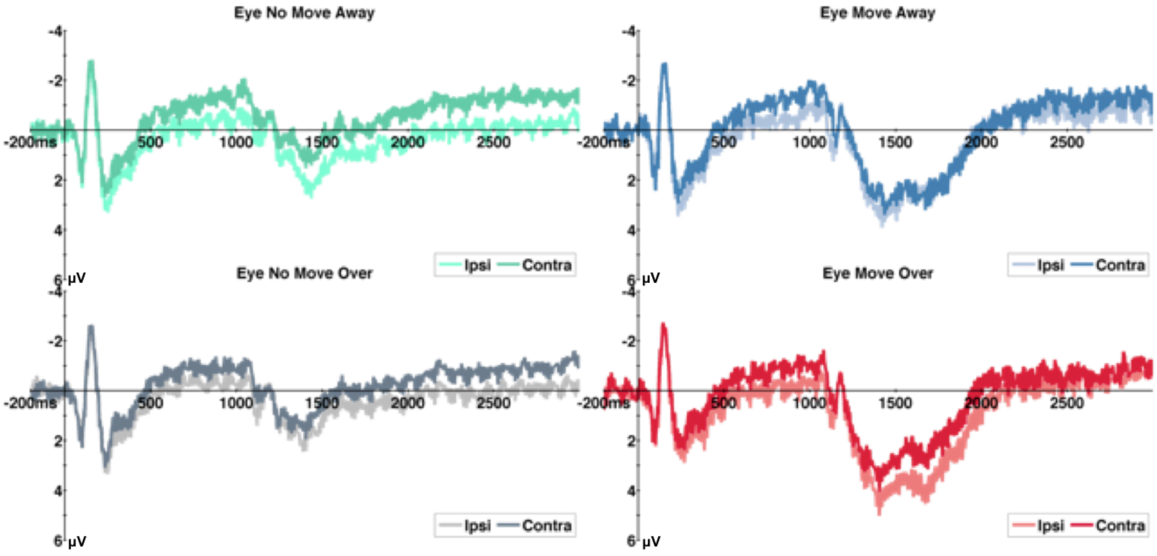

Figure 17. Contralateral and ipsilateral activity for Experiment 2
Contralateral and ipsilateral activity at the average of posterior electrode sites after ICA.

Experiment 3

In the past experiments, with the lateralized change detection task that is used to measure the CDA, we have confounded the spatiotopic and retinotopic coordinate systems. Participants have usually fixated the center of the screen whereby the left side was always the left side of the screen as well as the left side of where the participants look. With building evidence that the visual system frequently operates in retinotopic coordinates, we sought to find the coordinate system used by the CDA for maintaining items in VWM.

With Experiment 3 we tested whether the CDA was based within retinotopic or spatiotopic coordinates. If the CDA is only sensitive to spatiotopic coordinates then the electrophysiological activity would be the same in both conditions. However, if as we suspect, the CDA is based in retinotopic coordinates, then the condition where participants fixated laterally before the onset of the memory array would show the exact same activity in the opposite polarity (if we hold the definition of contralateral constant across conditions). This finding would help to validate our interpretations of the previous experiments' results.

Behavioral results

Participants performed the working memory task with mean accuracy about 87.43% (*SD*=4.89%). Trials where the participant did not correctly respond to the working memory test were not included in the final analysis (*M*=5.13%, *SD*=4.89%).

Eye tracking results

Although participants were cued to move their eyes before the onset of the memory to a particular fixation cross, we used the same time windows of interest to ensure that the participants were maintaining fixation at the beginning and towards the end of the trial. The average percent of trials rejected for participants fixating outside of target area during the time windows of interest was 17.79% (*SD*=10.38%).

Electrophysiology results

The central fixation condition, which is similar to standard working memory tasks that require the participant to maintain central fixation, shows a sustained CDA across the length of the trial (Figure 18). There is also a comparatively larger visual evoked response in both conditions compared to Experiments 1 and 2, which is consistent with using a unilateral stimulus display in Experiment 3.

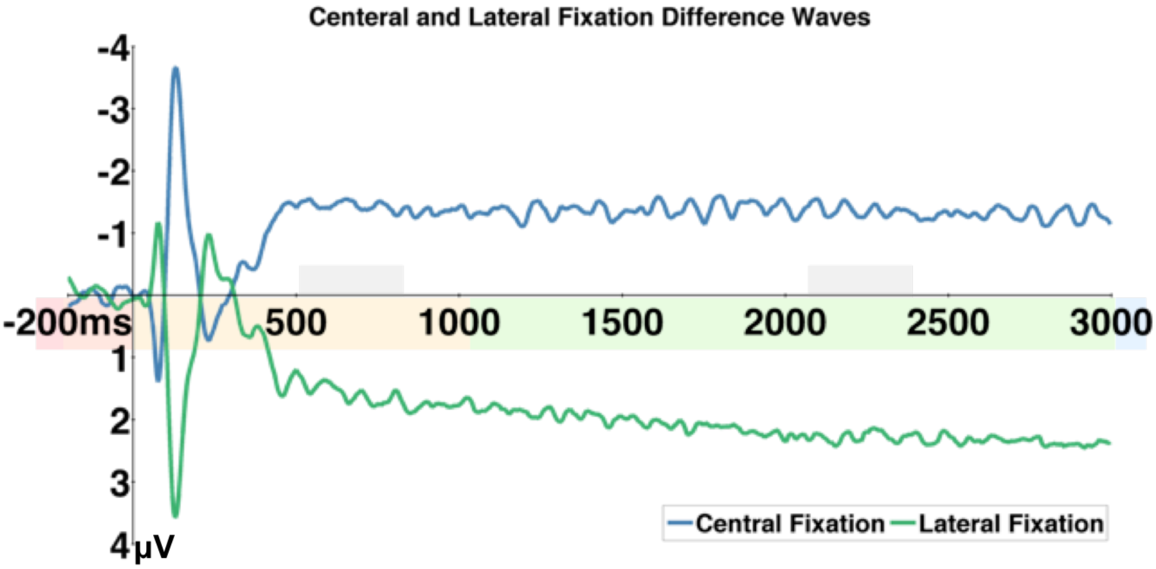

Figure 18. Contralateral – ipsilateral difference waves for Experiment 3
CDA calculated as the difference waves for contralateral – ipsilateral activity at the average of posterior electrode sites.

In comparison, in the lateralized fixation condition, where participants moved their eyes before the onset of the memory array so that the items would appear in the opposite visual hemifield at onset, we see a sustained activity identical to the CDA, just in the positive polarity (Figure 18). This is consistent with the CDA being based in retinotopic coordinates. This finding helps validate our interpretations of the previous experiments' results.

DISCUSSION

Experiment 1 showed that if the contents of attention changes then the VWM representations remap almost immediately to stay contralateral to the updated focus of attention. This is consistent with what is seen with tasks that have used abrupt onset stimuli such as the classic Duhamel, Colby, & Goldberg (1992) study. In particular, we showed it was possible to track shifts of attention between visual hemifields through flips in polarity of the CDA, with a static display, extending the findings of the MOT literature (Drew et al., 2014). As we had predicted, the CDA remained contralateral to the currently attended items.

However, the eye movement condition revealed an unexpected and massive ramp up in negative activity around the time of the eye movement that was sustained throughout the trial. Despite the eye movement drawing the items into the opposite visual hemifield, similar to the attention condition, there was no sign of a flip in polarity. This experiment showed preliminary evidence for an eye movement related signal that could be measured with ERPs. This signal was contralaterally organized, leading us to suspect an additive relationship with the eye movement related activity and the CDA.

Experiment 2 replicated and extended these findings by having participants move their eyes over and away from the attended side, resulting in leftward and rightward attention trials with eye movements of equal distance magnitude but in opposite directions. Using this paradigm we confirmed that the eye movement related component was contralaterally organized, and unlike the HEOG, with the polarity of the activity determined by the direction of the eye movement relative to the focus of attention. Examining the difference waves, eye movements toward the attended visual hemifield resulted in negative activity, while eye movements away from the attended visual hemifield resulted in an approximately equal amplitude component, but in positive polarity. Therefore, when we averaged the activity together for the Eye Move Over and Away conditions the activity associated with the eye movements of opposite directions but equal distance averaged out, revealing the underlying CDA.

After teasing apart this contralateral eye movement activity from the underlying CDA we found that the VWM representations of the items were sustained in the original contralateral hemisphere for several hundred milliseconds following an eye movement, while a representation is slowly formed in the other hemisphere. As revealed by examining the contralateral and ipsilateral activity separately, when eye positions changed, a representation was maintained in the hemisphere contralateral to the original memory array onset, while ipsilateral activity eventually increased so that both hemispheres hold a representation of the items by the end of the trial. A similar effect is revealed in the eye move over condition, where the attended visual hemifield is switched following the eye movement, when independent components related to horizontal eye movement artifacts are removed. This finding may have parallels in the saccadic remapping literature; however, our focus is on the sustained item representations held in VWM and proposing that the contralateral eye movement activity may help us keep track of where the eyes are moved relative to where attended items are encoded.

When we then take the subtractions from Experiment 1 for the attention condition and the subtractions from Experiment 2 for the average of the eye move conditions, although we cannot make direct statistical comparisons because the results are not from within the same sample of participants, we can at least see that the amplitude of the remapped activity in the eye subtraction is close to half that of the attention subtraction. This is consistent with our finding that the contralateral activity remains throughout the length of the trial while the ipsilateral activity rises to maintain the representation over time. This is also consistent with expectations of remapped responses reaching about half the magnitude of visual responses (Merriam, Genovese, & Colby, 2003).

Finally, Experiment 3 supplemented our findings by confirming that the CDA operates within retinotopic space. Although this was assumed in the past literature, within the context of the present experiments where every finding is underpinned by a complex system of contralateral and ipsilateral, it is important to know whether this is with respect to retinotopic or spatiotopic coordinate systems.

IMPLICATIONS AND FUTURE DIRECTIONS

VWM can aid in maintaining representations of items in sustained attention when items are still present in our environment and in memory when the items either disappear, shift in the environment as in multiple object tracking, or when we move our eyes. All of the representations can also be tracked by the CDA using ERPs in humans, providing for direct comparisons in future research. We found evidence for sustained VWM item representations following eye movements in the original encoding hemisphere, while a secondary representation builds in the ipsilateral hemisphere. One potential future direction of this research would be to investigate the mechanisms and ramifications of holding a representation in both hemispheres at the same time. Perhaps there is increased coherence between the hemispheres, the activity becoming in phase as they start to share the representation. Are two separately generated representations created that can then be compared to reduce the error of the remembered features of the items? For example, this could result in more precise VWM resolution. Such a benefit would not be found for maintaining two representations in Experiment 1 for the attention move condition, as the items being held in memory are different in each hemisphere. Maintaining the originally encoded items while creating the representations for the other visual hemifield could lead to memory errors. Instead, the original representations in the contralateral hemisphere are dropped. When new representations are created that provide a more accurate representation of the current visual input the representations can be updated rapidly, rather than lingering over time.

Although one can draw parallels with the spatial remapping and saccadic remapping literature, the present findings may reflect a long chain of events that occur as a consequence of an eye movement. Furthermore, since our findings are being measured at the scalp level in humans we may be measuring a higher level, cognitive process. Previous studies examining remapping across saccades in humans using ERPs have had fundamental differences in their methodologies that complicate drawing comparisons. Such studies examined the activity time-locked to the onset of the saccade (Bellebaum & Daum, 2006; Bellebaum, Hoffmann, Daum, 2005; Peterburs, Gajda, Hoffmann, Daum, & Bellebaum, 2011). In our present tasks, participants were performing a working memory task and we were interested in the effects of eye movements on the working memory representations, therefore we time-locked to the onset of the memory array, to capture the CDA before and after the saccade was initiated.

The present paradigms also do not provide evidence for prospective remapping, although modifications of the task where there are sudden onsets of stimuli, or the participants can predict that an eye movement must be made, which would be closer to the tasks used with non-human primates that have shown such evidence (Duhamel, Colby, & Goldberg, 1992). In contrast, when an object is tracked across the vertical meridian between visual hemifields, the CDA has shown signs of predictive remapping across hemispheres, suggesting it is sensitive to the time course needed to reveal such effects (Drew et al., 2014). We also see a sustained representation in the original contralateral hemisphere throughout the trial; however, it is possible that with enough time or when an update is required that the representation could be dropped from the contralateral hemisphere and be predominately represented in the ipsilateral hemisphere.

The human visual system recruits and interacts with far reaching areas of cortex to construct our conscious perception of our environment across each shift of our gaze. Multiple times per second our brains must hold onto previously processed details and update it with new information across saccades while filling in the gaps between end points of our eyes' trajectories. VWM and attention may play vital roles in maintaining this information in an online format that allows further processing while allowing for a sense of stability. The present paradigms and findings suggest a potential mechanism whereby encoded representations are held in the brain where they are originally encoded, unless updates to the contents of attention are required, while secondary representations build elsewhere over time. This could allow for a steady and gradual transfer of information between hemispheres.

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