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The Neural and Oculomotor Correlates of Covert Spatial Attention

By

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DISSERTATION

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Abstract

The relationship between covert spatial attention and the oculomotor system remains a central topic in cognitive neuroscience, particularly regarding the functional role of microsaccades—small fixational eye movements once considered to be stochastic noise. This dissertation investigates whether microsaccades serve as an overt index of covert attention and how they modulate early visual processing in humans. Grounded in the Premotor Theory of Attention, which posits shared neural substrates for attentional shifts and saccade planning, the present research comprises three visual-spatial cuing studies utilizing simultaneous high-resolution eye-tracking with eye-position-contingent stimulus presentation and electroencephalography (EEG).

Study 1 (Chapter 2) examines microsaccade dynamics across two experiments varying in cue predictiveness: one utilizing high-validity (80/20) predictive cues and another using non-predictive (50/50) cues. The results demonstrate that predictive cues systematically modulate microsaccade rate, amplitude, and direction, eliciting a robust bias of microsaccades toward the attended location during the rebound period, the characteristic increase in eye movements following initial stimulus-induced inhibition. Conversely, non-predictive cues fail to produce these systematic biases, suggesting that microsaccades reflect top-down endogenous attentional engagement rather than purely reflexive orienting.

Study 2 (Chapter 3) investigates the neurophysiological associations of these movements by analyzing visual event-related potentials (ERPs) and event-related alpha-band oscillations based on microsaccade direction. In the predictive condition, congruent microsaccades (directed toward the target) were associated with enhanced contralateral P1 and N1 attention effects, and significant desynchronization of contralateral alpha power. Notably, no consistent attentional modulation was observed during congruent microsaccades for the C1 ERP component associated

with processing in primary visual cortex (V1). These findings support the majority view that spatial attention modulates human visual processing primarily in extrastriate cortex rather than V1, even when potentiated by oculomotor planning.

Study 3 (Chapter 4) addresses individual differences by exploring whether visual working memory (VWM) capacity predicts the strength of these attention-oculomotor interactions. High-VWM individuals exhibited superior behavioral performance and robust P1/N1 modulation on trials with congruent microsaccades, whereas Low-VWM individuals did not show these benefits. These results suggest that the coupling between microsaccades and attentional facilitation is dependent on executive control resources necessary for maintaining a stable spatial priority map.

Collectively, these findings provide some evidence that microsaccades function as a probabilistic index of covert attention that facilitates sensory processing in extrastriate visual areas. This dissertation elucidates the complex interplay between executive control, oculomotor mechanisms, and sensory gain, supporting an integrated view of the dorsal attention network where motor preparation and attentional selection are functionally intertwined.

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Chapter 1: Introduction

What is attention? As William James once said, “Everyone knows what attention is... It is the taking possession by the mind in clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought.” James, often called the Father of American psychology, devoted an entire chapter on attention when many contemporaries did not concern themselves with such a topic (James, 1890). James said, “Millions of items of the outward order are present to my senses which never properly enter into my experience. Why? Because they have no interest for me. My experience is what I agree to attend to”, which is largely the underlying concept of early theories of attention (see Historical background).

While James’ initial thoughts on attention provided a clear and intuitive description, more modern conceptualizations have expanded the scope of his original ideas. For instance, Buschman and Kastner (2015) defined attention as: “... the selective prioritization of the neural representations that are most relevant to one’s current behavioral goals”, and that the need for this prioritization is due to a limited capacity of cognitive resources. However, some have argued that such a unitary definition of attention does not benefit the scientific community and instead should be described in terms of the proposed underlying mechanisms (Brigard, 2012; Hommel et al., 2019; Luck & Vecera, 2002). Similarly, Buzsáki (2020) argued for the removal of “folk psychology” terms such as attention, and to describe processes based on observed neural mechanisms (but see Poeppel & Adolfs, 2020 for rebuttal). Although attention is a supra-modal process that influences all sensory modalities this dissertation focuses on visual attention.

In this next section, I review seminal early studies that illustrate the basic approaches in the modern attention literature, emphasizing how foundational issues have been presented in competing theories and empirical findings. Next, I review physiological theories of attention and

how individual and populations of sensory neurons are thought to be modulated by attention, followed by a more detailed discussion of the broad categories of attention and the underlying neural generators of these attention-related networks. Lastly, I consider the debate about how early, and at what perceptual processing stages, attention can modulate visual processing, and whether small eye movements known as microsaccades may in potentiate covert spatial attention during early vision.

Historical background

The modern study of attention can arguably be traced to Colin Cherry, who in 1953 published his seminal work on dichotic listening, known as the ‘cocktail party effect’. In these dichotic listening tasks, participants would typically wear headphones and listen to two distinct messages, one in each ear, and were instructed to ‘shadow’ or repeat back the words from just one of the two messages. Cherry reported that listeners could correctly report that the unattended audio message contained human speech, and a change from a male voice to a female voice, as well as a pure tone. However, the listeners could not discern any specific word or phrase, nor that the unattended audio message was spoken in English, and many (though not all) believed a reversed speech (containing no semantic content) to be normal. Interestingly, much of this research came out of necessity during wartime (particularly WWII), as pilots were having a difficult time listening to many different messages from their commanding officers while trying to attend to multiple air traffic control instructions over a single loudspeaker (see Kantowitz & Sorkin, 1983), and so it is perhaps not surprising that Cherry (1953) was supported in part by the Signal Corps, the Air Material Command, and the U.S. Office of Naval Research. One key takeaway from Cherry’s work is that our ability to focus on information in the environment is limited; we cannot take in and fully process everything that we hear, see and feel. In other words,

perception is 'selective', and research in this area came to be referred to as "selective attention" (Driver, 2001).

Broadbent (1958) used many of the foregoing observations to formulate his influential filter theory, which posited that, due to limited cognitive resources, a filter would act in a two-stage manner. It would first extract all physical properties of a stimulus (such as pitch or location of a sound) in a parallel fashion, and then in a second stage, more complex properties of the stimulus would be extracted. However, due to limited cognitive resources, this second stage would be conducted in a serial manner.

However, some of Broadbent's original hypotheses seem not to hold up to further scrutiny, as later studies found that listeners can use meaningfulness to follow a message back and forth between two ears (Gray & Wedderburn, 1960). Deutsch and Deutsch (1963) and later Norman (1968) offered an alternative model, the late selection theory, in which they proposed that the bottleneck for limited cognitive resources is not at the stage of perceptual processing, but instead is due to a limitation of the response system. They proposed that humans can perceive many simultaneous messages, but that the response system is limited in that it can only, in the case of the dichotic listening tasks, respond to one stream of stimuli at a time.

Separately, Treisman (1960) presented listeners with a meaningful message that would at some point switch to a random sequence of words, while the other ear's message would begin with meaningless words and would switch simultaneously as the other ear to meaningful content. What was observed was that some listeners would continue to shadow the meaningless content, while others would switch the ear they would shadow to attend to the meaningful content. How could this pattern of switching be explained if, as Broadbent's early selection model proposes,

semantically complex information from the unattended ear is filtered out prior to higher-level processing?

To reconcile these discrepancies in Broadbent's (1958) original filter theory of attention and include consideration of the findings of Deutsch and Deutsch (1963), Treisman (1964) proposed her attenuation theory of attention (a variant of early selection theory), in which some stimuli (in this case auditory) would be weakened, or attenuated, but that they would not be completely filtered out, as in Broadbent's theory. However, semantic selection criteria would apply for both ears, so that if your name is mentioned in a crowded room while you are engaged in another conversation (the so-called "cocktail party effect"), you can still hear your name, though it will be much harder, as the signal is attenuated (though not entirely filtered out as proposed by Broadbent). Thus, the ability to hear your name while engaged in another conversation in a crowded room appears to stem from the attenuation, but not complete filtering, of the physical properties of the stimulus.

In 1967, Treisman and Geffen conducted a study to pit the early and late selection theories against one another. By having listeners shadow one message while simultaneously listening to both messages for a key word, they were able to parse out the differences between the two theories such that, if the target word the participants were listening for was detected equally well in the shadowed and ignored ear, this would be evidence in favor of Deutsch and Deutsch's (1963) late selection model of attention. However, their findings supported Treisman's (1964) attenuation (and thus an early selection) theory of attention, in that participants detected 87% of the key words in the shadowed ear while only detecting 8% in the ignored ear. One characteristic of Treisman's theorizing that continues to have relevance in more recent

formulation of selective attention is the notion of attention working as an attenuator (or alternatively as an accentuator) of some stimuli but not others.

Attention in the Visual domain

Following the early studies of selective attention in the auditory modality described above, much work has focused on visual attention, in line with the significant advances in vision science. Much of this research has focused on attention to locations in space (see section on Posner cueing paradigm below). Such research has taken advantage of chronometric measures such as reaction time as dependent variables. For instance, researchers can measure response latency to a peripheral target when a preceding flash cues the correct location versus an incorrect one (Posner, 1980; Posner, Nissen, & Ogden, 1978). In this regard, one avenue of research split attention into two broad categories: voluntary (also called endogenous) attention and involuntary (exogenous) attention. While in the spatial domain the former is typically studied with symbolic cues (often centrally located), exogenous (or reflexive) attention studies typically presents the cues in the to-be-attended location directly (Jonides, 1981; Kustov & Robinson, 1996). Further, it was recognized that while exogenous attention involves bottom-up processing of environmental stimuli that are automatic and reflect more sensory information, endogenous attention requires top-down cognitive control, in order to maintain the relevant, goal-directed behavior that is most suitable for the current situation (Corbetta & Shulman, 2002). As described above, it is often best to discuss visual attention in terms of task-related mechanisms so as to not confuse different aspects of attention with one another.

Visual search

Some of the first experiments done in visual attention were visual search tasks, which require participants to search for and respond to a target stimulus among an array of distracters. For instance, Neisser (1964) had participants search for the letter 'K' and recorded the times it took to find the target in an array. Because the letter 'K' is similar in feature (color, size, shape) relative to other neighboring stimuli (letters), this search must be done serially, or item by item. However, if for instance the 'K' was instead presented in red while all other neighboring distracters were green, the 'pop-out' nature of the single red 'K' would make the search much faster, and could be done in a parallel fashion (Treisman & Gelade, 1980). Interestingly, in this same experiment, participants were separately asked to search for a 'T' in an array of 'I' and 'Z' letters, but were almost twice as slow at responding during this task compared to the simple 'pop-out' feature task, presumably because the target 'T' shared multiple features as the other two distracter 'I' and 'Z' letters. This led Treisman to describe what is now known as the 'binding problem', which concerns how multiple features in the visual field can be integrated within perception to produce distinct objects. For instance, if a blue square and a red triangle are in the visual field, and neurons are firing for each of those two colors, as well as the two shapes, how does the brain combine the features of these objects, so that what results is not a red square and a blue triangle? In contrast, if a blue square appears in the visual field alone, those features can be assumed to come from that single object. To address this, Treisman and Gelade (1980) proposed their seminal Feature Integration Theory (FIT) of attention, which stated that each object presented simultaneously in the visual field must be attended to in order to perceive and thus integrate those features into a single object. This is contrasted to a pop-out scenario such as

previously describe, in that the single unique feature can be oriented to without the need for serial search.

Another finding from visual search tasks is the observation that participants are slower at searching (moving our eyes) a previously just-searched location compared to a novel location, a phenomenon known as inhibition of return. For example, a participant who searches for a target at location A, then B, will have a harder time re-searching location A compared to a new location, C. This phenomenon is thought to facilitate seeking new areas that may contain the target of interest, while hindering the ability to reinvestigate an already known location.

Posner Cueing Paradigm

Early work by Eriksen and Hoffman (1974) established that spatial cues systematically reduce reaction times compared to uncued or neutral stimuli. Building off this concept, much of our understanding of spatial attention comes from Michael Posner and the subsequent use of his cueing paradigm. In 1980, Posner published his seminal work on orienting attention, in which he used what is now called a Posner cueing paradigm to study the orienting of attention in the visual domain. A key aspect of the paradigm is that participants are instructed to maintain their eyes on a centrally located fixation point—a dot or plus sign—and to use covert spatial attention to attend to peripheral target stimuli. By dissociating eye gaze from attentional shifts he isolated covert (internal) attention from overt attention involving eye movements to attended locations in space. Posner presented participants with either a plus sign indicating a 50/50 chance the task-relevant target would appear on either side (and thus was uninformative) or a left or right sided arrow which indicated the target would appear on that side 80% of the time; these were called valid trials. The other 20% of the time the arrow would incorrectly predict the location of the target; these were called invalid trials (see Figure 1.1, left). As shown on the right side of Figure

1.1, participants were faster to press a button to the valid target stimuli than the invalid one. Reaction times in neutral (uninformative cue) trials fell between these two conditions, indicating an intermediate level of facilitation. This pattern, known as the Posner cueing effect, is interpreted as the behavioral benefits and costs—compared to neutral trials—of pre-allocating attention to one hemifield or having to reorient attention from one hemifield to the other, respectively. This robust finding seems to hold true not just for simple choice reaction time tasks, but also for both choice spatial and choice symbolic tasks. However, with behavioral measures such as accuracy and reaction time it is challenging to infer the underlying neural processes contributing to the attention cuing effects.

By using methodologies such as electroencephalography (EEG) and event-related potentials (ERPs) to measure neural processing it is possible to better understand the neural mechanisms of covert spatial attention. Such methods thus help address the debate as to whether attention works in an early or late selection manner. I will return to the topic of electrophysiological measures of spatial attention after a review of the literature on the neural underpinnings of attention.

Attentional Effects at the Neuron Level

Neurophysiologists have long been in pursuit of the neural underpinnings of attention (Hernandez-Peon et al., 1956; Hubel et al., 1956). Because monitoring the activity of individual neurons or small populations of neurons requires invasive brain techniques, much of this work has used nonhuman primates (Buschman & Kastner, 2015). While there is much evidence (and thus scientific consensus) that attention acts to increase the overall neuronal response to stimuli at attended locations (or attended features) compared to unattended (e.g., Nobre & Kastner, 2014; Petersen & Posner, 2012), the underlying mechanisms of such biasing remains debated.

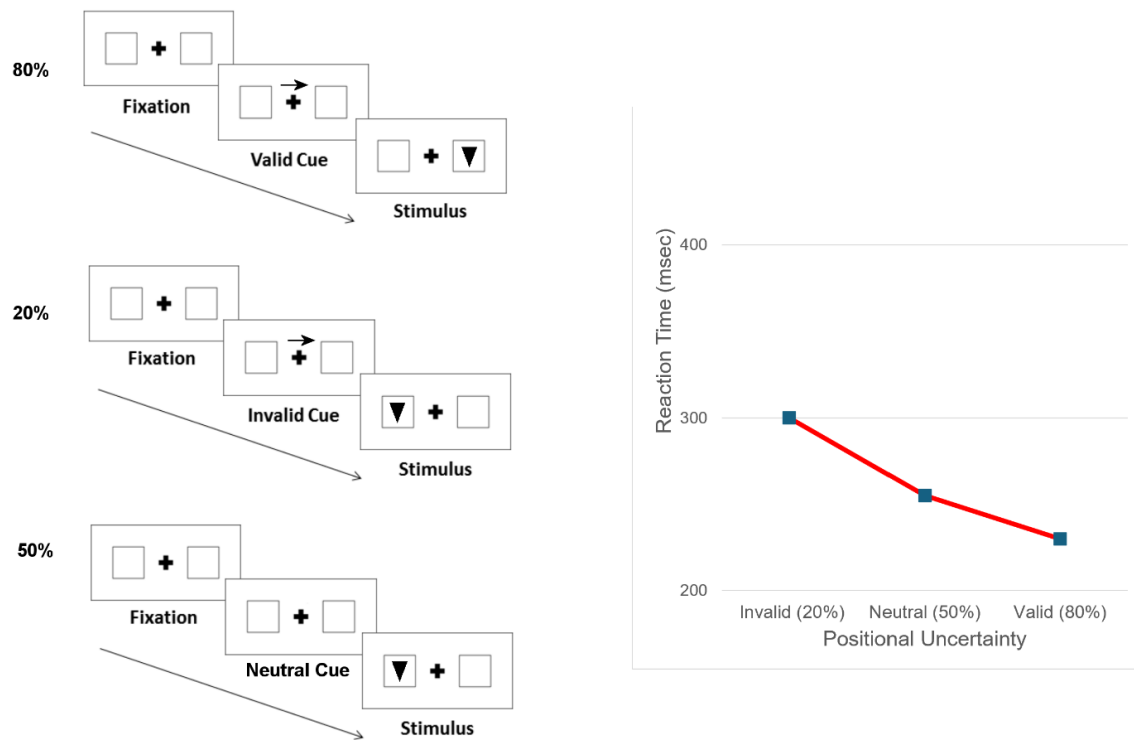


Figure 1.1. (left) Posner cueing paradigm (right) RT results in the Posner paradigm.

To investigate these mechanisms, Bushnell and colleagues (1981) implanted electrodes into posterior parietal cortex of four monkeys, who completed both a peripheral-attentional task in which the monkeys detected a peripheral visual stimulus while holding fixation centrally, as well as a task that required the monkey to reach for a stimulus and touch it. In both cases, directing attention toward the receptive field of a single parietal cortex neuron increased its firing rate in response to the stimulus, demonstrating in nonhuman primates that even single neurons can exhibit attentional modulation. Given this evidence, it may seem obvious that spatial attentional modulation acts by increasing the response rate of neurons. However, this appears to be not the only effect, and there is evidence that spatial attention also acts to increase the sensitivity of single neurons (Martínez-Trujillo & Treue, 2002; Reynolds, Pasternak, & Desimone, 2000).

McAdams and Maunsell (1999) recorded single-unit activity from primary visual area (V1) and V4 neurons in two monkeys that engaged in a match-to-sample task (the latter visual area being of primary interest). While maintaining central fixation, the monkeys pressed a lever which would cause the presentation of two sample stimuli, located in an attended and unattended location. After the disappearance of the sample stimuli, two test stimuli would appear in the same locations, which signaled the monkeys to release the lever (that they had been pressing since the initial fixation) if the attended-location test stimulus matched the sample stimulus that appeared in the same location. At one location, the stimuli were Gabor patches, which the monkeys had to match the orientations, while at the same time isoluminant colored Gaussian patches were presented in the other location. When instructed (via training) to attend to one location the monkeys were required to match the color. While the Gabors were placed within the V4 receptive fields, the colored Gaussians were not, and as such, the authors deemed ‘attended’ trials those that instructed the monkeys to attend to the orientation of the Gabors, while the ‘unattended’ condition consisted of color-match trials, since that location was outside of the V4 RFs and thus these neurons only responded preferentially to the Gabors (orientation match condition). Crucially, the authors plotted the normalized V4 population response rate for the attended and unattended conditions and found a near perfect correlation, suggesting that attention causes a proportional change in the evoked response. McAdams and Maunsell (1999) interpreted these observations as evidence that attention acts to multiplicatively scale neuronal output.

However, this multiplicative scaling theory does not explain some empirical evidence. For instance, Moran and Desimone (1985) similarly recorded V4 neuronal response in monkeys engaged in a match-to-sample task, and demonstrated that two competing stimuli presented in the same V4 receptive field resulted in a decreased response at that site, presumably due to

competition with one another. However, when attention was directed to one of the two stimuli within the same RF, the neuron responded only to the attended stimulus, showing one of the first examples of how two simultaneous stimuli compete for attentional resources within early visual areas (the biased competition model of attention).

Based on the idea that attention acts to bias competition between stimuli towards the attended side, Desimone and Duncan (1995) proposed that bottom-up signals from early visual areas may be interacting with top-down control signals from higher order areas. More specifically, it was proposed that attention acts as a top-down signal to bias activity toward neurons that preferentially respond to the stimulus's spatial location and features, and that these neurons are then enhanced so they have a competitive advantage over others.

Another study by Luck and colleagues (1997) implanted electrodes in visual areas V1, V2, and V4, in two macaques. The monkeys were taught to hold fixation centrally while peripherally attending to one of two locations (in the absence of a trial-by-trial visual cue). The authors chose nontarget stimuli that the visual regions of interest would preferentially (or not) fire to those orientations and color. These nontarget stimuli, in one variation of the task, were presented sequentially, so that only one nontarget stimulus appeared at a time, while in another variation, the two nontarget stimuli (one in the attended, one in the unattended location) would appear simultaneously. After nontarget stimuli sequences, a target square was presented in the attended location, to which the monkey was required to release a lever. They observed that when the two nontarget stimuli were simultaneously presented in the same receptive field, both V2 and V4 firing rates were modulated by attention, such that the attended effective stimulus elicited greater firing rates than the ineffective stimulus. However, no attentional modulation was observed in V1, largely because the receptive fields of V1 were too small to contain both stimuli.

In 2009, Reynolds and Heeger proposed their divisive normalization model of attention, which posited that the evoked-response at each neuron will be divided by the sum response from that population of neurons, thus ‘normalizing’ the response of any individual neuron. Behaviorally, this would answer many of the questions as to how the visual system can respond to and perceive such a wide range of visual stimuli (for instance, how would the visual system be able to detect a candle far in the distance at night, but also be able to search for a friend on a bright day in Times Square?). More importantly, this model would reconcile seemingly mutually exclusive theories of attention, particularly response gain function theories (McAdams & Maunsell, 1999; Williford & Maunsell, 2006), competition bias theories (e.g., Moran & Desimone, 1985), as well as contrast-response function theories (e.g., Martínez-Trujillo & Treue, 2002), the latter of which the normalization model of attention was based on (Reynolds et al., 2000).

The normalization model of attention consists of three main subcomponents: the stimulation field, the suppressive field, and the attention field. The stimulation field, as the authors put it, is essentially the neuron’s receptive field, without suppression or attention, which characterizes its selectivity to spatial locations or features such as orientation. In turn, the suppressive field is the amount of suppression allocated to surrounding distracters, such as unpreferred spatial locations or orientations. Lastly, the attention field is characterized by its gain for each neuron in a population, and is factored into the equation before normalization, so that both the stimulation and suppressive fields are used to determine the output firing of the population of neurons.

For example, if two stimuli are presented in a neuron’s receptive field, but one stimulus is the cell’s preferred orientation while the other is not, only the former contributes to the stimulus

drive, while both contribute to the suppression field. In turn, the response of this neuron is less compared to if the preferred stimulus was presented alone. If attention is directed toward the preferred stimulus in the RF, the stimulus drive increases and the balance between excitation and suppression shifts toward the preferred orientation, thus resulting in an increased firing rate of that neuron. The normalization model of attention is mostly concerned with local attentional mechanisms, and in the following sections I will review studies and theories looking at attention from a broader perspective.

On a more global level, it is thought that attention may act to modulate other interconnected brain regions through effective connectivity by altering the synchrony of such neurons. This has been referred to as Communication Through Coherence (CTC; Fries, 2005). By timing the peaks of depolarization of many neurons across two interconnected regions, information is thought to be most efficiently passed from one region to another, and this is thought to be a mechanism in which attention can flexibly and rapidly change depending on current behavioral goals (Bosman et al., 2012). While much of CTC theory has been implemented into mathematical models (see Tiesinga & Sejnowski, 2010), there is some empirical evidence to support this theory. For instance, when two groups of neurons are active, Womelsdorf and colleagues (2007) found that their strength depends in part on their coherence. Likewise, they observed that neurons in group A may be in phase with those in group B, but group A and group C are not in phase, demonstrating the selective nature of these rhythms.

Dorsal Attention Network (DAN)

In 2002, Corbetta and Shulman proposed their seminal theory that the visual system is controlled by two ‘partially segregated neural systems’: the ventral attentional network (see below) and the dorsal frontoparietal network. The dorsal frontoparietal network, which primarily

consists of the frontal eye fields (FEF), intraparietal sulcus (IPS), and to a lesser extent the middle temporal complex (MT+) and superior parietal lobule (SPL), is thought largely to play a role in voluntary selective attention, and more specifically, covert spatial attention in which a peripheral stimulus is anticipated at a specific location, both in humans and in non-human primates (Corbetta & Shulman, 2002). Similar mechanisms seem to play a role in object/featural attention. For instance, Shulman and colleagues (1999) presented participants with an arrow cue that would indicate the direction (left or right) a subsequent array of dots would be moving among a second array of distracters. Because what was cued was not location but the motion of the dots, participants had no spatial information to use. Despite the lack of cue-related spatial information, a similar frontoparietal network was seen as during spatial attention tasks. Lastly, while the dorsal frontoparietal network is largely mediated by top-down selection, bottom-up information appears to influence discriminability. When a monkey makes a saccade to an oddball target during a visual search task, FEF neurons discriminate between the target and distracters (Thompson, Bichot, & Schall, 1997), and this effect is also observed when monkeys covertly attend, suggesting it is not related to the eye movements, per se. Crucially, however, is that because the color of stimuli were counterbalanced (targets sometimes were green and distracters were red, and vice versa), bottom-up sensory information was likely the biggest factor in this discriminability. In terms of object recognition, the lateral intraparietal area (LIP) and FEF neurons may be involved in generating salience maps, which combine both top-down and bottom-up information to best select the object of interest (Wolfe, 1994).

Ventral Attention Network (VAN)

In contrast to the DAN, the ventral attention network (right ventral frontoparietal network or VAN as Corbetta and Shulman, 2002 call it), which includes the temporoparietal junction

(TPJ) cortex and the ventral frontal cortex (VFC), appears to be largely involved in the reorienting of attention toward behaviorally-relevant goals that are outside of the current locus of attention. Given its right-hemispheric specialization, this system has large implications in terms of unilateral lesions typically observed in neglect patients which is likely one of several deficits contributing to the overall behavioral problems in patients with this disorder. To contrast the functional differences between the DAN and VAN networks, activation was plotted for the IPS and FEF (DAN-related regions) and the TPJ (VAN related) in response to a cue indicating the likely direction of motion of the upcoming stimulus array (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000). While IPS and FEF were activated during the cue and through the cue-target-interval (CTI) until the target onset, indicating an attentional set for this cue-target relationship, while no similar activation was observed for TPJ. However, TPJ cortex showed significantly more activity when the participants needed to reorient to the target when it was presented at the invalidly cued location (Corbetta et al., 2000). While originally believed to be specific for reorienting spatial attention, evidence has shown VAN activation when unexpected stimuli are presented at central fixation (Marois, Leung, & Gore, 2000), or when unexpected stimuli appear at attended locations (Kirino, Belger, Goldman-Rakic, & McCarthy, 2000).

Eye Movements

Unlike many animals, most mammals have the ability to rapidly reorient the visual system by moving the eyes within the eye socket in order to train the highest acuity portion of the retina (the fovea) on the visual information of interest. Many other species must rely on less mobile eyes or overt head movements, requiring much more energy and time. The rapidness of the reorienting of the visual system via eye movements can be best observed in nonhuman

primate studies, in which monkeys are trained to respond with an eye movement toward a target location (e.g., Willeke et al., 2019).

Four classes of eye movements are of interest in primates: smooth pursuit, vergence, vestibulo-ocular reflexive movements and saccades (both large and small - Gegenfurtner, 2016; Kowler, 2011). This dissertation focuses on the latter, saccadic eye movements.

Saccades

Saccades are ballistic eye movements that rapidly move a peripheral stimulus closer to the fovea in a series of jerky “step-like” motions (Gegenfurtner, 2016). These voluntary eye movements occur very rapidly and simultaneously in both eyes and are thought to need as little as 80 ms of cortical processing to be initiated (Kirchner & Thorpe, 2006). Saccades allow for a relatively small retinal region of high visual acuity—the human fovea is approximately 2 degrees of visual angle—to be brought to bear on objects of interest. They can occur rapidly, quickly reorienting gaze as many as three or four times a second (Schotter, Angele, & Rayner, 2012). Despite being one of the primary mechanisms to quickly explore an environment, saccades actually impair vision both before and during a saccade (Ross, Morrone, Goldberg, & Burr, 2001). This is largely due to saccadic suppression that inhibits incoming visual information during eye movements (Burr, Morrone, Ross, & Zeno, 1994). Saccadic suppression avoids registering the very blurry image that would accompany high speed saccades (Burr & Ross, 1982).

To explain where humans look in a visual scene, Koch and Ullman (1985) proposed their seminal notion of ‘saliency maps’, which proposed that bottom-up physical features such as luminance, orientation, color, and motion would draw the eyes, rather than higher-order object properties *per se*. The idea of saliency maps has been updated to incorporate some aspects of

top-down control (Itti & Koch, 2001). For example, the concept of “meaning maps” posits that gaze is drawn to semantically-relevant regions of a scene (Henderson & Hayes, 2017).

Microsaccades

Studies of eye movements also examined the eyes while an observer was maintaining fixation on a target (e.g., Kowler, 2011). Such studies employed a bite bar to stabilize the head, and often used a contact lens optical lever to track the eyes, which had a very precise resolution as small as a few seconds of arc (one second of arc is equivalent to $1/3600^{\text{th}}$ of a degree of visual angle). One finding from these studies was that the eyes are rarely entirely still, but instead make small movements roughly 15 minutes of arc (0.25° of visual angle) simultaneously in both eyes, and that these occur every few seconds in some individuals, and up to three times per second in others (Collewyn & Kowler, 2008; Steinman, Haddad, Skavenski, & Wyman, 1973). These tiny eye movements are known as **microsaccades**, sometimes called fixational eye movements.

While more recent studies have demonstrated microsaccades occur during more naturalistic conditions such as when the head is free to move (not constrained by a bite bar or chin rest; e.g., Ferman, Collewyn, Jansen, & Van den Berg, 1987), the characteristics of these microsaccades (pattern, velocity, variability of eye position) was altered.

Historically, microsaccades were thought to be functionally different from larger saccades and were viewed as likely detrimental to vision due to retinal smearing (Steinman et al., 1973), though it is now generally accepted that they share the same characteristics as larger saccades, including the same neural generators (Hafed et al., 2021). Whereas saccades as described above are thought to facilitate the exploration of the environment by rapidly relocating the fovea to meaningful locations in the field of view, microsaccades may not serve a similar function. For instance, threading the needle and rifle-shooting experiments have demonstrated

that microsaccade rates actually decrease during these intensive visual tasks (Ko, Poletti, & Rucci, 2010; Winterson & Collewun, 1976). One further functional distinction is that there is evidence that microsaccades help to prevent retinal adaptation to stimuli (Martinez-Conde, Macknik, Troncoso, & Dyar, 2006).

Typical Microsaccade Dynamics

Microsaccades are typically defined as movements less than 1° of visual angle that occur binocularly at a specific velocity, often $6^\circ/\text{s}$ (e.g., Engbert & Kliegl, 2003; Møller, Laursen, Tygesen, & Sjølie, 2002). They exhibit a robust "main sequence" relationship, where peak velocity is linearly correlated with amplitude, a hallmark of the saccadic system that persists even at the microscopic scale (Bahill et al., 1975; Engbert, 2006; Martinez-Conde et al., 2013; Møller et al., 2002; Otero-Millan et al., 2008; Zuber et al., 1965). In the absence of a visual target, microsaccades typically occur at a rate of approximately 1–3 Hz (Engbert & Kliegl, 2003; Martinez-Conde et al., 2013; Rolfs, 2009). However, the onset of a visual cue initiates a stereotypical microsaccade rate signature, characterized by an abrupt suppression of generation (microsaccadic inhibition) starting less than 100 ms post-stimulus (Engbert & Kliegl, 2003; Rolfs, 2009; Rolfs et al., 2008). This inhibition phase is thought to reflect a phase resetting of ongoing oculomotor rhythms by the sensory onset (Tian et al., 2016). This is followed by a microsaccadic rebound at approximately 200–400 ms, where the rate increases above baseline before returning to steady-state frequency (Engbert & Kliegl, 2003; Galfano et al., 2004; Rolfs, 2009; Rolfs et al., 2008).

Microsaccades and Covert Spatial Attention

More recently, interest has been focused on the idea that microsaccades may not be totally random. It has been shown that microsaccades tend to be directed toward the location of a

one-sided arrow cue during modified Posner cueing paradigms (Engbert & Kliegl, 2003). In fact, it has been proposed that, during covert spatial attention, eye movement control areas in the brain generate small pre-saccadic activity during preparation for a full-blown saccade, and that this activity occurs even when an eye movement never occurs. This is known as the Premotor Theory of Attention (Kustov & Robinson, 1996; Sheliga, Riggio, & Rizzolatti, 1994, 1995). Support for this theory comes from Kustov and Robinson (1996), who demonstrated that the endpoints of saccades evoked by electrical micro-stimulation of the superior colliculus (SC) were systematically deviated in the direction of a covert spatial cue. Crucially, the temporal profile of these deviations matched the source of the attentional shift: peripheral cues caused reflexive deviations at short delays, whereas central symbolic cues required longer delays to produce similar motor deviations, indicating the engagement of top-down cortical control (Krauzlis et al., 2013; Kustov & Robinson, 1996). This suggests that even when no overt eye movement is produced, the shift in priority influences activity in the motor map, biasing the oculomotor system.

Complementary behavioral evidence by Sheliga, Riggio, and Rizzolatti (1994) showed that covertly attending to a location causes the trajectory of a subsequent saccade (aimed at a different location) to curve away from the attended site (Sheliga et al., 1994; Sheliga et al., 1995). This interference suggests that the oculomotor system is actively engaged during the attentional interval, maintaining a suppressed saccadic plan toward the cued location.

Similarly, Hafed and Clark (2002) postulated that microsaccades might be an index of covert attention, as they observed better accuracy early in trials when a microsaccade was directed toward the target stimulus compared to later in the trial when microsaccades were directed away from the target. Likewise, when controlling for retinal eccentricity, human

participants were more accurate on a perceptual discrimination task when a spontaneous microsaccade was made towards versus away from a peripheral target (Yuval-Greenberg, Merriam, & Heeger, 2014). Others have observed similar accuracy benefits (Liu, Nobre, & van Ede, 2022). In terms of reaction time benefits of microsaccades, there is less consensus. Some groups have reported a benefit in RT when microsaccades are directed toward the cue but not the target (Horowitz, Fine, Fencsik, Yurgenson, & Wolfe, 2007; Laubrock, Engbert, Rolfs, & Kliegl, 2007; Meyberg, Sinn, Engbert, & Sommer, 2017), while others (Laubrock, Kliegl, Rolfs, & Engbert, 2010; Liu, Nobre, & van Ede, 2022) have found a decrease (albeit small) in reaction times if the first or last microsaccade was made in the direction of the target (Srinivasan, Lowet, Gomes, & Desimone, 2025).

The mechanistic origin of these microsaccade biases has also been a point of rigorous investigation. In a 2024 study, Liu and colleagues addressed whether shifting attention creates new microsaccades or merely biases the direction of the ongoing ones (Liu, Alexopoulou, & van Ede, 2024). By comparing attention-directing retro cues to sensory-matched neutral cues, the researchers found no increase in the overall rate of microsaccades following the cue, despite the presence of robust directional modulations. This implies that shifting attention does not trigger a motor command in the traditional sense. Instead, it rebalances the neuronal activity within subcortical structures like the superior colliculus. When a microsaccade happens to occur due to the endogenous rhythms of the oculomotor system, its direction is simply biased toward the attended location by the skewed neural landscape. Thus, microsaccades appear to be probabilistic as opposed to deterministic: covert attention shifts do not trigger the generation of new microsaccades but rather bias the direction of naturally occurring, ongoing microsaccades.

Neural Circuitry of Microsaccades

There is evidence that eye movement generation and the allocation of spatial attention share similar neural circuitry, most notably the SC (Hafed, Goffart, & Krauzlis, 2009) and superior frontal cortex including FEF. These regions contain populations of neurons that exhibit both sensory visual responses and movement-related discharges (Bruce & Goldberg, 1985; Wurtz & Goldberg, 1972).

Superior Colliculus (SC)

A critical feature of the SC is its topographic map of visual and motor space, characterized by significant foveal magnification (Azzopardi & Cowey, 1996). Although the fovea constitutes only about 10% of the visual field, nearly one-third of the SC surface area is devoted to this region (Buonocore, Tian, Khademi & Hafed, 2021). This overrepresentation underscores the SC's pivotal role in fine-grained oculomotor control.

Recent neurophysiological evidence has overturned the notion that this map is bifurcated into "fixation" and "saccade" zones. Instead, research suggests a single, continuous representation of displacement vectors where the foveal zone serves as the primary substrate for generating microsaccades (Hafed, Chen, & Tian, 2015; Hafed & Krauzlis, 2012). All classic properties of the SC observed during large saccade generation remain intact for microsaccades (Hafed, Yoshida, Tian, Buonocore, & Malevich, 2021).

Structurally, the SC is organized into superficial (SCs) and intermediate/deep (SCi) layers (Krauzlis et al., 2013; White & Munoz, 2011). While the SCs primarily handles bottom-up visual processing, the SCi integrates these signals with top-down commands from FEF and LIP. Neurons within the SCi exhibit "build-up" activity proportional to the probability of target selection (Glimcher & Sparks, 1992; Munoz & Wurtz, 1995). This reflects a competitive

"winner-take-all" process mediated by lateral inhibition, where top-down signals bias population-level activity toward the covertly attended coordinate (Basso & Wurtz, 1998; White & Munoz, 2011).

Frontal Eye Fields (FEF)

While the SC provides execution signals for microsaccades, FEF acts as the cognitive control hub, maintaining reciprocal connections with extrastriate areas (e.g., V4) and providing descending projections to the SC (Anderson, Kennedy, & Martin, 2011; Schall, 2002). Within the FEF, a heterogeneous population of neurons is classified based on response properties: **visual neurons** modulate attention to stimulus onset; **motor neurons** fire exclusively during saccade execution; and **visuomotor neurons** exhibit both sensory responses and preparatory activity (Gregoriou et al., 2012). This functional diversity corresponds to distinct anatomical segregation. Neurons providing top-down feedback to the visual cortex are predominantly located in supragranular layers (2/3), whereas those projecting to the SC—the primary motor output of the attention network—reside exclusively in infragranular layer 5 (Fiebelkorn & Kastner, 2020; Pouget et al., 2009).

Crucially, the rostral region of the SC serves as a prerequisite for microsaccade generation. During steady fixation, rostral neurons exhibit sustained firing that transitions into a phasic burst approximately 100 ms prior to movement onset (Hafed & Krauzlis, 2012). This transition represents the stochastic release of the microsaccade program; reversible inactivation (e.g., via muscimol) silences this activity and significantly reduces microsaccade likelihood (Hafed, Lovejoy, & Krauzlis, 2013).

Electrophysiological Studies of Visuospatial Attention in Humans

Mangun and Hillyard (1991) had participants engage in a Posner cueing paradigm in which a central arrow cue would indicate the probable location of the upcoming target (75:25 validity), after which a bar stimulus would appear, and the participants had to discriminate bar heights. The participants responded with a button press with either hand to indicate whether the bars were large (left button) or small (right button). As shown in Figure 1.2, they reported a posterior increase in the P1 component (90-130 ms post-stimulus) to validly-cued but not invalidly-cued stimuli contralateral to the visual field in which the stimuli were presented. Likewise, a negative N1 component (150-200 ms post-stimulus) was larger (more negative) over contralateral posterior electrode sites when attention was directed toward the target (valid trials) compared to the unattended (invalid) trials. However, participants also completed a simple RT task, in which they pressed one button as soon as they saw the target, in which case the P1 effect, but not the N1 effect, survived (not shown). The authors attributed this dissociation between the two visually-evoked potentials (VEP) to a likely difference in task difficulty, though this difference must be component-specific, as the P1 did not differ between tasks. More recent follow-up has revealed that the N1 attention effect is likely due to a discriminative process, based on the observation that it can be greatly attenuated with a simple RT task (involving no discrimination; e.g., Vogel & Luck, 2000). Because this attentional modulated increase in P1 occurred roughly 100 ms post-stimulus, but average reaction times were closer to 554 ms (for valid trials), this data supports the notion of an early selection attentional mechanism, as the attentional modulation appears to occur before the selection of the response (see Luck,

Woodman, & Vogel, 2000 for a review on evidence supporting late selection theories in ERP data).

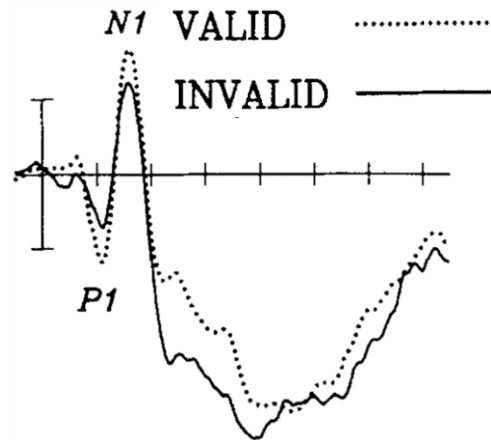


Figure 1.2. Adapted from Mangun & Hillyard, 1991; note y-axis (negative

Early on, these findings led to the theories of sensory ‘gain control’, largely due to the finding of an enhanced P1 for attended compared to unattended stimuli (Hillyard & Anllo-Vento, 1998). However, if attention acts to increase the gain of the signal, the gain would also increase any noise associated with the signal, thus not improving the attended signal in any meaningful way (see Luck et al., 2000). To address this, a modified theory was proposed, which explained two different types of noise: internal neural noise and external stimulus noise (Lu & Doshier, 1998). It was proposed that attention amplifies the stimulus noise without influencing the neural noise, thus leading to improved behavioral performance (Hawkins et al., 1990).

Following this, many studies have attempted to locate the neural generators of the P1 and N1 components, often using a combination of magnetic resonance imaging (MRI), current source density maps (Mangun, Hillyard, & Luck, 1993), BESA source dipole modeling (e.g., Di Russo, Martínez, Sereno, Pitzalis, & Hillyard, 2002), or positron emission tomography (Woldorff et al., 1997). These data suggest a dorsal extrastriate cortex generator for the early portion of the P1

wave, while the later portion appears to have a source in the ventral fusiform gyrus. The N1, however, appears to be comprised of at least two subcomponents (Luck, 2014), which further complicates its theorized sources. One point of evidence that multiple underlying neural generators may be contributing to the scalp N1 is that its broad distribution (ranging from occipital, posterior, temporal, and even more anterior regions) makes it unlikely that it is one or two generators (as appears to be the case with P1). Further, the latency differences of N1 at different scalp regions (as much as 15 ms faster onset for parietal electrodes compared to occipital-temporal sites) points to varying generators (Mangun, 1995).

Another attention-related ERP component, the N2-posterior-contralateral (N2pc), is a negative deflection around 200-300 ms post-stimulus observed over lateral posterior electrode sites and is named because it is larger in contralateral electrodes compared to those ipsilateral in relation to the visual stimulus (Luck & Hillyard, 1994). This component can be used to measure covert attention and reorienting, by subtracting the contralateral-ipsilateral activation, and much converging evidence has pointed to a neural generator near the lateral occipital complex, and in some situations, visual area V4 (Hopf et al., 2006; Hopf, Vogel, Woodman, Heinze, & Luck, 2002). While originally thought to reflect distracter suppression (Luck & Hillyard, 1994), it now appears the N2pc is much more complicated, but is related to resource-limited allocation of attention to a target, but that is influenced by distracters (Ester, Drew, Klee, Vogel, & Awh, 2012).

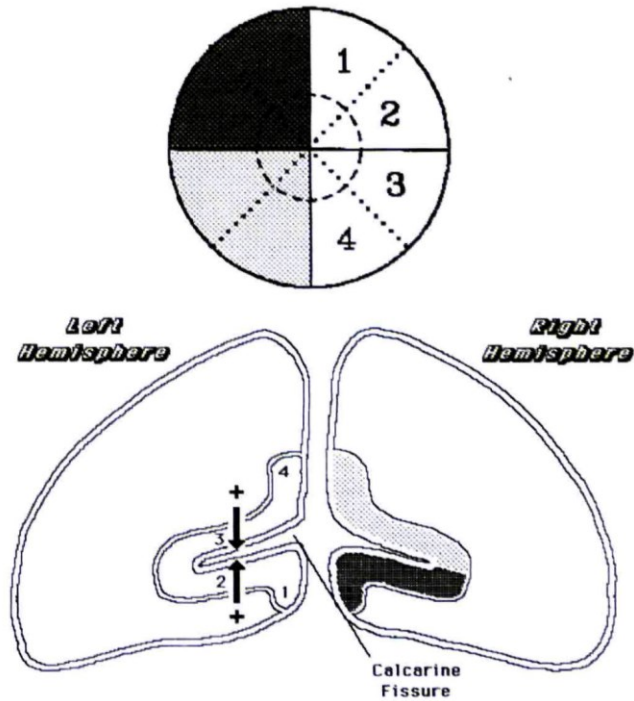


Figure 1.3; adapted from Mangun, 1995

Lastly, the C1 component (50-90 ms post-stimulus) is the first VEP, which is best seen over posterior midline electrodes (see Slotnick, 2013). Similar to previously described components, there has been a large effort to uncover the neural generator of C1, sometimes called NP80 (see Mangun, 1995), which now appears to have a source in primary visual cortex (e.g., Di Russo et al., 2002). Initial evidence that the C1 component originates from striate cortex is that, roughly in line with the retinotopic topography of the calcarine fissure (see Figure 1.3), C1 inverses polarity based on the visual hemifield in which a stimulus is presented, characteristic of V1's cruciform shape (Kelly & Mohr, 2018). For instance, upper visual field stimuli elicit a negative C1 deflection, while lower visual field stimuli result in a positive C1 deflection (Jeffreys & Axford, 1972 – see Figure 1.4). More recently, a combination of MRI and dipole modeling has further supported the claim that C1 is largely generated in striate cortex (Clark, Fan, & Hillyard, 1995; Di Russo et al., 2002; Mangun, 1995; Martinez et al., 1999).

How Early Does Spatial Attention Modulate Visual Processing?

As discussed above, it appears (e.g., Nobre & Kastner, 2014; Petersen & Posner, 2012) that spatial attention acts to selectively enhance the attended information early in the visual processing stream. However, the question remains as to how early and where in the visual processing stream does this take place?

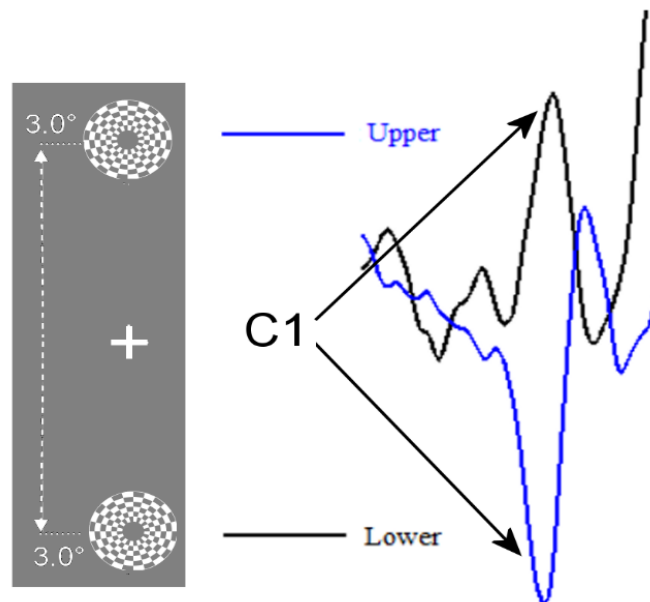


Figure 1.4. C1 ERPs from upper and lower visual field stimuli at the POz electrode site.

As early as 1984, Francis Crick proposed that the sharing of visual information between different visual regions, such as the lateral geniculate nucleus in the thalamus and primary visual cortex, may be mediated by ‘cell assemblies’, in which the firing *pattern* of neurons, not the

individual specificity of distinct neurons, would be the critical information of a firing neuron. Since then, researchers have employed designs to investigate how early and at what stages visual processing can be modulated by spatial attention.

For instance, Motter (1993) conducted an experiment in which they recorded activity transdurally in the cortex in order to investigate attentional modulation in the earliest visual cortical regions. For about one-third of the recorded neurons, they observed an increase in V1 firing rates when attention was directed toward a stimulus in the neuron's receptive field (RF) compared to when attention was directed away. More critically, however, was the observation that of the attentionally-modulated neurons, 67% of them only showed the effect when more than one competing stimulus was within the visual field.

More recently, several studies investigating this question in nonhuman primates have similarly supported the idea that spatial attention may modulate visual processing as early as striate cortex (Gandhi, Heeger, & Boynton, 1999; Somers, Dale, Seiffert, & Tootell, 1999; Tootell et al., 1998). Even more striking is the finding that attention may modulate visual information even earlier than the input to primary visual cortex, as early as lateral geniculate nucleus (Briggs, Mangun, & Usrey, 2013; McAlonan, Cavanaugh, & Wurtz, 2008).

However, in 1999, Martinez and colleagues set out to investigate when and where in the visual hierarchy does attentional modulation occur. Participants were centrally-cued with a non-predictive (50% chance) left or right arrow, after which an array of '+' signs bordered either an upright 'T' (86% of trials; nontarget), or an inverted 'T' (14% of trials; target). The participants made a button press when the target (inverted T) appeared within these arrays. When the participants selectively attended to the targets, there was an increase in the BOLD signal in V1 contralateral to the attended visual field, compared to when the targets appeared in the

unattended visual field. Furthermore, the experiments found the activations at retinotopically parafoveal locations, which corresponded to the locations of the stimuli. Similarly, they observed spatial attention modulations in V2, V3, and V4v. Additionally, because of the poor temporal resolution of the BOLD signal, the authors collected ERPs to have a sense of the timing of these early visual area modulations. While classic attention-related ERP effects such as a larger P1 and a more negative N1 for the attended compared to unattended arrays was observed, there was no spatial attention modulation of the early visual C1 component, which as reviewed above is thought to reflect feedforward visual information from V1 into higher-order visual areas (Slotnick, 2013). Due to these discrepancies, the authors postulated that the spatial attention modulations seen in the BOLD signal may arise from a feedback signal from higher visual areas, but not the feedforward signal from V1.

To further investigate whether this was truly a feedback signal from higher visual areas, or instead, may be due to a top-down biasing signal that results in prolonged activation of V1 that does not directly impact the feedforward signal, Martínez and colleagues (2001) conducted a follow-up study using a very similar design as previously described. By modeling the C1 dipole, they demonstrated that while there was no C1 attentional modulation (similar to their previous finding), a later attention-related effect, beginning around 160 ms after target onset, arose and lasted for roughly 100 ms within the same calcarine source. Interestingly, these delayed signals have also been observed in the magnetic-equivalent, event-related fields (e.g., Noesselt et al., 2002). In this vein, many researchers have since utilized ERPs due to their millisecond-scale temporal resolution (Nunez & Srinivasan, 2006) in order to further elucidate whether these apparent V1 attentional modulations are indeed acting on a delayed feedforward signal, or instead a feedback signal from higher cortical areas.

The Majority View

In the past two and a half decades, many resources have been poured into this question of how early attention can modulate visual areas. Recently, there has been an attempt to make sense of the wide-ranging studies on this topic, many of which found no selective spatial-attentional modulation of the early VEP C1 (Baumgartner, Gaulty, Hillyard, & Pitts, 2018; Clark & Hillyard, 1996; Di Russo, Martinez, & Hillyard, 2003; Di Russo et al., 2012; Ding, Martinez, Qu, & Hillyard, 2014; Fu, Caggiano, Greenwood, & Parasuraman, 2005; Fu et al., 2008; Hopfinger & West, 2006; Johannes, Münte, Heinze, & Mangun, 1995; Mangun et al., 2001; Martinez et al., 1999; Martínez et al., 2001; Wijers, Lange, Mulder, & Mulder, 1997). This has been termed the ‘majority view’, as much of the overall literature appears to favor the idea that attentional modulation does not occur as early as the afferent feedforward sweep of visual information from V1 into higher cortical visual areas (see Slotnick, 2018a for review). For instance, Di Russo and colleagues (2003) had participants perform a cueing paradigm in which they were instructed to maintain central fixation and were cued either to the left or the right in either the upper visual field *or* the lower visual field (upper and lower visual field stimuli were presented in separate blocks; see Figure 11). There was no difference in C1 amplitude or latency at a posterior midline site when the targets were attended to compared to unattended. However, a positive P1 beginning around 120 ms and lasting until around 160 ms post-stimulus was significantly greater for the attended versus unattended targets, as well as a slightly later (~170-220 ms post-stimulus) N1, which was likewise larger (more negative) for attended versus unattended trials. While the C1 effect, or lack thereof, along with further evidence from the ‘majority view’ points toward no spatial attentional modulation as early as primary visual cortex, V1, this study confirms the now canonical attention-related P1 and N1 effect that has been

replicated numerous times before (see Mangun, 1995), demonstrating attention was allocated to the left and right visual fields as expected.

The Minority View

While much of the evidence to date supports the notion that attentional modulation does not occur until extrastriate cortex (P1 or later in terms of ERP components), there is conflicting evidence that indeed spatial attention can influence visual processing as early as striate cortex (the C1 component serving as proxy). These studies have been grouped into the ‘minority view’, since many fewer studies have reported evidence in support *for* attentional modulation at this early processing stage (Dassanayake, Michie, & Fulham, 2016; Fu et al., 2009; Kelly, Gomez-Ramirez, & Foxe, 2008; Rauss, Pourtois, Vuilleumier, & Schwartz, 2012; Rauss, Pourtois, Vuilleumier, & Schwartz, 2009). However, in one study in particular, Kelly and colleagues (2008) have made a compelling case for C1 attention effects. They first had participants complete a ‘probe’ session in which they presented Gabor gratings (6 degrees per cycle) in one of eight locations 4° away from fixation to elicit the largest C1 response in that individual, due to the individual differences in striate cortex (calcarine fissure *per se*) folding patterns as previously described. These locations were to be used in for a modified Posner cueing paradigm, and the experimenters chose the locations diagonal from each other for each participant (i.e., locations 1 and 5).

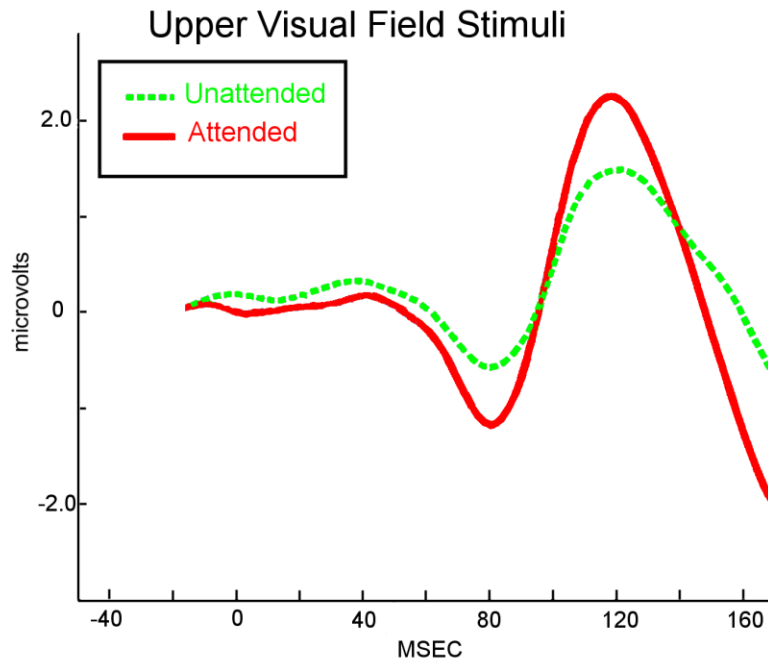


Figure 1.5. Based on Kelly et al (2008)

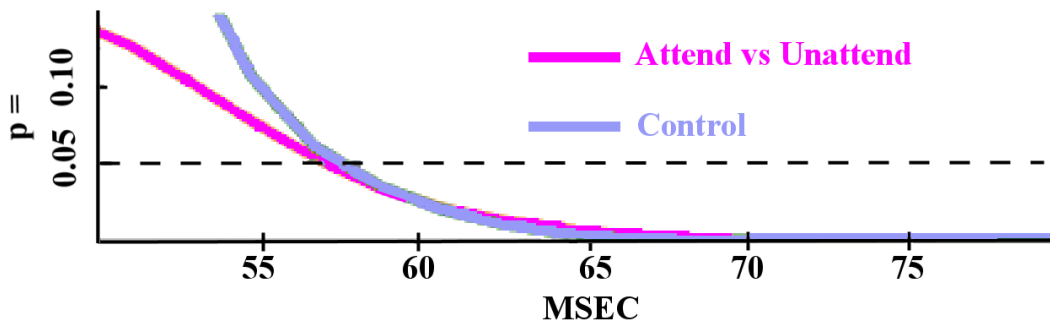


Figure 1.6. Based on Kelly et al (2008)

During the visuospatial task, participants were instructed to maintain central fixation, and were non-predicatively cued to one of the two box outlines which served as target placeholders via an L-shaped cue. Occasionally (30% of trials), target trials were presented consisting of the standard Gabor patch superimposed with a dark ring inside, to which participants made a button response. Crucially, participants only responded to valid trials, and ignored invalid trials. When

stimuli were presented in the upper visual field (Figure 1.5), there was a negative C1 peaking around 80 ms post-stimulus, which was larger (more negative) for attended versus unattended stimuli. A similar, inverted, effect is seen for stimuli presented in the lower visual field (not shown). As was discussed previously (e.g., Mangun, 1995), Kelly et al also found an attention-related P1 effect (~120 ms post-stimulus), in which attended stimuli elicited a larger P1 component compared to unattended stimuli. Strikingly, when stimuli were presented in the lower visual field, the C1 component appeared to have merged with the P1, not only eliminating the ability to statistically test this difference, but also (statistically insignificantly) seems to push the latency of the C1 peaks ~10 ms later. To ensure this early activity was indeed the C1 instead of some interaction between the former and a P1 component, the authors compared the onset latency in the probe task to that during the visuospatial task. As can be seen in Figure 1.6, which plots the time-course of when the probe statistically differed from the baseline activity (thus showing the time-course of the onset of C1 without attention conditions) and the attention effect, when the attended and unattended conditions statistically. That these two time-courses matched was taken as evidence that this attentional difference is indeed during the C1 time-course.

Why the Discrepancies?

One remaining question, however, is: why are there so many disparate findings, which are seemingly mutually exclusive? One reason may be due to the different methodological approaches each study has taken. For instance, in one review (see special issue in *Cognitive Neuroscience*, 2018, edited by Slotnick), it is suggested that in order to elicit a robust C1, the study should: use a design that maximizes attentional and perceptual load (see Lavie, 1995), employ distracters (see Desimone & Duncan, 1995), elicit attention exogenously, and balance the contrast in that, while perceptually difficult to see, the stimuli are not too dim as to not elicit

a C1 (Fu, 2018). Additionally, Slotnick (2018) proposes that measurements should be taken at posterior midline electrode sites, specifically to avoid contamination of C1 with lateral P1 and N1 components, and to avoid confounding the C1 with P1 by utilizing upper visual field stimuli. However, as Kelly and Mohr (2018) note, these suggestions are based on the handful of ‘minority view’ findings Slotnick (2018) chose to review, omitting various other studies that employed different designs. Furthermore, many of the previous studies have employed varying parameters that are not included in (or are contradictory to) those described by Slotnick (2018), yet still found positive results. For instance, the design used by Kelly and colleagues (2008) as previously described employed no distracters and endogenously captured attention (both of which contradict Slotnick’s suggestions). Another reason for these discrepancies may be as simple as a type I error, in which we see false positive results in the literature (which generally would make sense, given the ratio of majority/minority view publications), though this seems unlikely given the statistical power in previous studies (Baumgartner et al., 2018). Another discrepancy may be the high inter-individual variability of V1 anatomy (Klein, 2018), which could dilute the statistical power of previous results if the locations of the stimuli are not varied by participant, as did Kelly and colleagues (2008). As will be reviewed in the following section, more recently there has been evidence to suggest that eye movements, and in particular microsaccades, may play a role in potentiating V1 attentional effects. In all the studies mentioned, eye movements as small as microsaccades were removed from the analyses, ensuring a stable image on the retina trial to trial, which in fact may be detrimental to spatial attention research.

Role of Microsaccades in Covert Spatial Attention?

Bouhnik, Korch, and Slovin (2025) investigated the neural mechanisms underlying pre-microsaccadic modulation in the foveal primary visual cortex (V1) using high-resolution voltage-sensitive dye (VSD) imaging. They recorded population-level neural activity from two awake, behaving non-human primates implanted with a recording chamber in V1. The animals performed a fixation task in which a small Gabor patch appeared at foveal eccentricities of 0.5°–1.5° while high-precision eye-tracking monitored spontaneous, uninstructed microsaccades. To isolate the neural correlates of motor planning and attention, the researchers categorized trials based on whether the microsaccade direction brought the gaze closer to (Toward) or further from (Away) the visual stimulus. They then analyzed the spatiotemporal dynamics of the VSD signals—reflecting aggregate membrane potential changes—at the retinotopic representations of both the current stimulus site and the future saccade landing site during the interval immediately preceding the onset of the microsaccade. They reported that spontaneous microsaccades were preceded by distinct, spatially specific modulation in V1 that predicted the direction of the upcoming eye movement. Specifically, they observed a significant ramping of population-level activity at the retinotopic representation of the current stimulus approximately 40 to 60 ms prior to movement onset, occurring in the absence of any external visual changes. Crucially, this pre-microsaccadic enhancement was contingent upon direction: V1 excitability increased significantly when the animal prepared a microsaccade directed toward the stimulus but was suppressed or absent during trials where the eye moved away from the target. Furthermore, the authors detected simultaneous activation at the foveal center—the future landing site of the saccade—suggesting a predictive remapping mechanism that anticipates the post-saccadic retinal image. This preparatory phase was characterized by a transient spike in synchronization between the neuronal populations representing the current stimulus and the future motor goal roughly 50

ms before the onset of the microsaccade, indicating that V1 plays an active role in the selection and planning of fixational eye movements.

In higher-order area V4, microsaccades toward an attended stimulus significantly enhance object representations and sharpen tuning curves (Srinivasan, Lowet, Gomes & Desimone, 2025). Research in macaques demonstrated that if the first microsaccade after an attentional cue is directed away from the target, the typical attentional enhancement of firing rates is delayed until the next microsaccade toward the cued stimulus. This indicates that microsaccades can reset or refresh the sensory response, playing a mechanistic role in initiating the effects of attention on cortical processing.

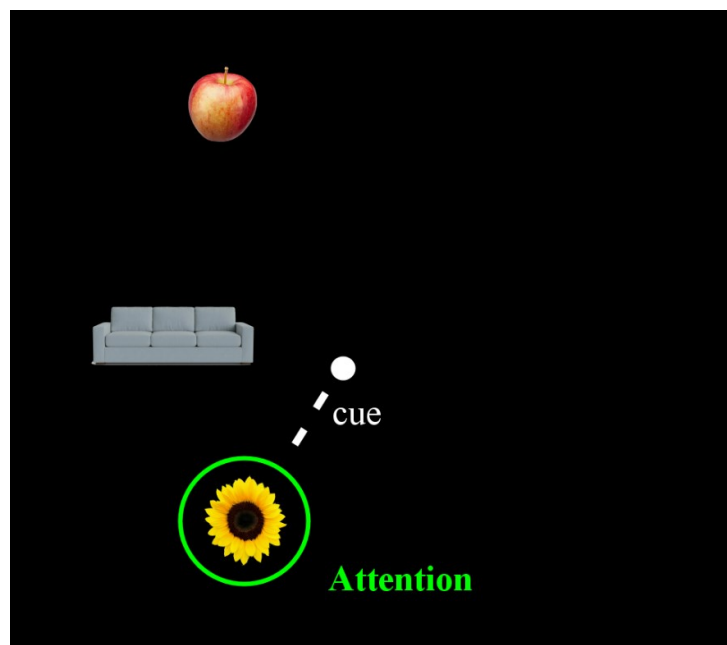


Figure 1.7. Based on Lowet et al (2018).

Similarly, Lowet and colleagues (2018) recorded eye position and multiunit activity in visual areas V4 and inferotemporal cortex (IT) from two monkeys who engaged in a visuospatial cueing paradigm, shown in Figure 1.7. The monkeys were trained to maintain central fixation while three stimuli would appear, one of which was cued with a dashed line toward it, and the monkeys would saccade to the target after a brief interval. Interestingly, when a microsaccade toward the upcoming target was made, V4 neurons in the receptive field had increased firing rates compared to the neurons outside of that receptive field (seen in Figure 1.8). Crucially, when a microsaccade was directed *away* from the upcoming target, no attentional modulation was observed for V4 firing rates, indicating microsaccades may *potentiate* covert spatial attention effects.

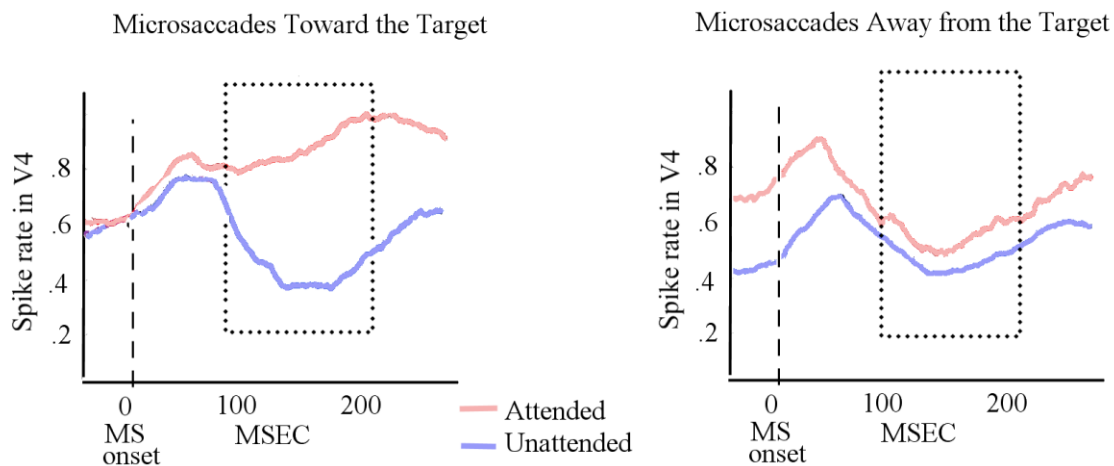


Figure 1.8. Based on data from Lowet et al., 2018

EEG Studies examining the role of Microsaccades in covert Spatial Attention

In a seminal 2022 study, Liu, Nobre, and van Ede examined the relationship between microsaccades and the lateralization of EEG alpha activity (8–12 Hz) during a task requiring covert spatial attention. In their experiment, participants memorized two lateralized items and,

following a delay, were cued by a central color change to select and report the orientation of one item from working memory. Using simultaneous high-speed eye-tracking and EEG, the researchers sorted trials based on the presence and direction of microsaccades during the attentional selection period (200–600 ms post-cue), categorizing them as toward, away, or no microsaccade trials relative to the attended memory item. The authors found that while microsaccades and neural alpha modulation are functionally correlated, the latter does not depend on the former. Specifically, alpha lateralization was stronger and reached its peak earlier in trials where microsaccades were directed toward the attended item compared to trials where microsaccades were directed away or occurred later. However, the critical finding was that “no microsaccade” trials still exhibited clear and robust spatial alpha lateralization that was statistically indistinguishable from trials containing attention-directed microsaccades. These results demonstrate that while directional biases in microsaccades are associated with covert attention, they are not a necessary prerequisite for the neural modulation of spatial attention to occur.

In a subsequent study, Liu, Nobre, and van Ede (2024) investigated whether spontaneous microsaccades, occurring during periods of attempted fixation without external incentives to shift attention, elicit transient lateralization of EEG alpha band activity (8–12 Hz). The authors analyzed simultaneous high-speed eye-tracking (1000 Hz) and high-density EEG data from 23 human participants during the retention delay of a visual working memory task—a period characterized by a static central fixation cross and no demand for lateralized spatial attention. Using a velocity-based detection algorithm, they isolated spontaneous microsaccades and categorized them based on their horizontal direction (left vs. right) and their kinematic function relative to the fixation target (“start” microsaccades moving gaze away from center vs. “return”

microsaccades correcting gaze back to center). The EEG data were then time-locked to the onset of these microsaccades to calculate time-frequency representations of spectral power and inter-trial phase coherence in lateral posterior electrodes (PO7/8).

This study revealed that the onset of spontaneous microsaccades was consistently followed by a robust, transient lateralization of posterior alpha activity that peaked between 0 and 250 ms. Specifically, alpha power was significantly lower in the hemisphere contralateral to the microsaccade direction compared to the ipsilateral hemisphere. This lateralization pattern was observed regardless of the microsaccade's kinematic function, appearing for both "start" microsaccades (shifting gaze away from fixation) and "return" microsaccades (shifting gaze back to fixation). Further analysis indicated that this lateralization index was driven predominantly by a burst of increased alpha power in the hemisphere ipsilateral to the microsaccade direction, rather than a suppression of contralateral activity. Additionally, the authors found that this ipsilateral alpha modulation possessed a strong phase-locked component, evidenced by a significant increase in inter-trial phase coherence within the alpha band, suggesting that the observed transient lateralization is partially constituted by the spectral footprint of the microsaccade-related potential.

The Current Dissertation Studies

The studies reported here explore the role of microsaccades in covert spatial attention in humans. Across the following three chapters, I analyze data from two datasets comprising behavior, eye-tracking, and EEG/ERP measures of visual-spatial attention investigated in trial-by-trial cuing paradigms. In Chapter 2, I present analyses of eye-tracking data to investigate whether the microsaccadic rate signature—defined by an initial period of stimulus-driven inhibition (<100 ms) followed by a post-suppression rebound—is sensitive to the informational

value of attentional cues (Engbert & Kliegl, 2003; Lv et al., 2022; Willett & Mayo, 2023). This analysis establishes the kinematic and temporal character of microsaccades, testing the notion they are an overt index of attention. In Chapter 3, I extend this analysis to determine how these microsaccadic metrics map onto concurrent neural activity as measured by EEG and ERPs (Engbert & Kliegl, 2003; Hafed & Clark, 2002; Liu et al., 2022; Liu et al., 2024). Finally, in Chapter 4 I investigate whether individual variations in visual working memory (VWM) capacity predict systematic differences in early visual attentional processes as modulated by microsaccadic dynamics (Gazzaley and Nobre, 2012; Guiliano, Karns, Neville, & Hillyard, 2014; Liu et al., 2022; Vogel & Machizawa, 2004). These associations are predicated on the theoretical grounds that VWM is not merely a passive storage buffer, but that it functions as a core executive process essential for the top-down control of selective attention (Gazzaley & Nobre, 2012; Kane et al., 2001).

Chapter 2: Study 1

Introduction

Spatial attention and eye movements are intimately connected in real world vision (Rizzolatti et al., 1987). Recent work has focused on the relationship between microsaccades and spatial attention, with evidence mounting that while the two are correlated they are not causally dependent on each other (Liu, Nobre & Van Ede, 2022). What remains a topic of interest is whether quantitative parameters of microsaccades, such as their rate, amplitude, and directional patterns are modulated with spatial attention.

Lv et al. (2022) is an example of prior work that investigated the effects of cue predictability (100%, 75%, and 50% validity) on behavioral performance and microsaccade

dynamics in a spatial cueing task emphasizing response accuracy. They used peripheral cues—brightening of markers at the left and right visual hemifield locations—thus confounding endogenous and exogenous attention effects. Behaviorally, they found a small (73% vs. 69%) but significant cueing effect on target accuracy in the 75% validity condition but not in the 50% condition. Consistent with the prior literature, microsaccade rate and amplitude exhibited characteristic temporal profiles following cue onset and before target presentation, including an early initial suppression, a rebound period, and a gradual return to baseline.

Critically, microsaccade dynamics were modulated by cue congruency and time after the cue. Microsaccade **rate** differed during the rebound period for congruent versus incongruent trials (microsaccade relative to cue direction), but this overall cuing pattern did not vary reliably across cue validity conditions. Microsaccade **amplitude**, however, showed stronger and more systematic cueing effects, with amplitudes biased opposite the cue direction during the rebound interval, consistent with inhibition of return. Additional amplitude modulations in the low-validity (50/50) condition suggested ongoing attentional shifts between potential target locations, which the authors interpreted as consistent with rhythmic attentional sampling, evident in the absence of strong top-down control. Importantly, only microsaccade amplitude during the rebound period—not rate—was correlated with behavioral cueing effects, indicating that microsaccade amplitude may more closely reflect the temporal dynamics of attentional allocation.

While this is a seminal study of spatial attention effects and their relation to microsaccades, several aspects of the study limit its interpretability. First, the use of peripheral cuing methods confounds endogenous and exogenous attention. Second, the methods emphasized accuracy over speed, and reaction times were not analyzed. Third, the probability

manipulation in the 75% produced modest attention effects on accuracy, and it is not clear, therefore, that the manipulation of attention was strong, perhaps owing to the simple target discrimination and absence of target masking, which together suggest that the perceptual load of the task may have been rather low (although the percent accuracy was not at ceiling). In addition, since subjects made microsaccades toward the targets, this means that effects on accuracy could have been confounded with changes in retinal eccentricity because the targets in congruent trials were closer to the fovea, albeit by a small amount, than on incongruent trials. Finally, the total numbers of trials in their single 40-minute session was limited, and this may have reduced the authors' power to detect attention cuing effects on microsaccades.

The present studies and analysis address unresolved questions arising from Lv et al. (2022) by isolating critical methodological factors, enabling clearer inference about the functional relationship between microsaccade dynamics and attentional processes. First, central arrow endogenous cues were used. Second, both speed and accuracy were emphasized, allowing for both RT and accuracy measures to be obtained. Third, the perceptual load of the target discrimination was increased by using a rapid pattern mask to obliterate iconic representations in order to eliminate the possibility that subjects ignore the cue and simply wait for the target to appear to shift attention. Fourth, and importantly, an eye-position-contingent stimulus presentation method was used to avoid the confound of retinal eccentricity and attention during microsaccades. Finally, the subjects were tested in two separate sessions to acquire a significant number of trials for analysis.

Overview of Design—The two experiments introduced in this chapter utilize high-resolution eye-tracking to characterize microsaccade dynamics, investigating how the strategic utility of a cue—whether it is predictive (80/20) or non-predictive (50/50)—modulates the rate, amplitude, and

directional patterns of these fixational movements across the cue-target interval in the Posner cueing paradigm (Engbert & Kliegl 2003, Laubrock et. al, 2005; Lv et al., 2022). Please note, the data in this chapter was gathered simultaneously with the EEG/ERP data described later in Chapter 3, but only the eye-tracking and behavioral data are reported here.

Participants engaged in an orientation discrimination task, in which they made speeded behavioral responses to target stimuli (square-wave gratings, 6 cycles/degree) presented randomly 4° to the right and left visual fields following a centrally-presented symmetric cue stimulus. In one experiment (Experiment 1a) the cue was a strong predictor of the correct location of the target (i.e., 80% valid cues and 20% invalid). In the second experiment (Experiment 1b), the cue stimulus was not predictive of the side of the upcoming target (50/50 probability). As mentioned above a crucial feature of the current experiments was to present stimuli in a gaze-contingent manner to control for changes in retinal eccentricity of the stimulus as a function of eye movements. This approach avoids confounds of cortical magnification on trials where a microsaccade is either made toward or away from the upcoming target stimulus.

The present analysis addresses whether the microsaccadic rate signature (described above) is sensitive to the informational value of the cue (Engbert & Kliegl, 2003; Lv et al., 2022; Willett & Mayo, 2023). More specifically, the objective is to determine if the goal-directed top-down control of attention that is recruited by predictive cues modulates the temporal profile of inhibition and/or facilitated rebound of microsaccades compared to the non-predictive case where attention is not selectively focused. If the results of Lv et al. (2022) are correct, then the pattern of MS dynamics in the current study should result in larger and possibly more MSs away from the cue, consistent with their inhibition of return explanation. However, finding more and

larger MSs in the direction of the cue would argue for a more typical attentional facilitation effect.

Finally, the inquiry addresses the behavioral consequences of these dynamics, investigating if the correlation between congruent microsaccades and reaction time (RT) facilitation is strictly contingent upon the strategic relevance of the cue (Hafed & Clark, 2002; Lv et al., 2022; Willett & Mayo, 2023).

The implementation of a binary cue validity manipulation facilitates the isolation of specific cognitive control mechanisms by contrasting two identical task architectures that vary exclusively in their informational entropy: a 50% valid (non-predictive) condition and an 80% valid (predictive) condition (Arjona et al., 2016; Lv et al., 2022; Olk et al., 2014; Posner, 1980). In the 50/50 non-predictive regime, the spatial cue possesses no strategic utility. Conversely, the 80/20 predictive regime introduces a substantial goal-directed component, requiring the subject to engage top-down, endogenous attentional resources to exploit the cue's strategic utility (Hein et al., 2006; Olk et al., 2014; Posner, 1980). This top-down engagement is evidenced by a distinct cost-benefit profile, where subjects exhibit significant response-time benefits on valid trials compared to neutral or invalid trials once they have committed processing capacity to the cued location (Luck & Hillyard, 1994; Mangun & Hillyard, 1991; Olk et al., 2014; Posner, 1980). The strategic utility of the cue is hypothesized to modulate the oculomotor system through the overlapping neural circuitry of the attentional and saccadic systems, specifically resulting in increased microsaccade rates and amplitudes for the predictive condition (Hafed et al., 2009; Lv et al., 2022).

Hypotheses—The primary hypothesis is that the strategic utility of spatial cues—operationalized through the contrast between 80/20 predictive and 50/50 non-predictive validity regimes—

systematically modulates the kinematic and temporal properties of fixational eye movements (Engbert & Kliegl, 2003; Lv et al., 2022; Willett & Mayo, 2023). Specifically, the prediction was that microsaccade rates and amplitudes would be significantly greater in the 80/20 dataset than in the 50/50 dataset. This is based on the idea that increased recruitment of top-down endogenous control resources (e.g., in the dorsal attention network) and a related potentiation of eye movement circuitry (e.g., FEF-colliculus) would influence attention-microsaccade coupling (Corbetta & Shulman, 2002; Hafed et al., 2009; Hafed et al., 2021; Peel et al., 2016).

It was also hypothesized that the directional bias of microsaccades during the cue-target interval would be stronger and more sustained in the 80/20 predictive dataset compared to the 50/50 non-predictive dataset (Lv et al., 2022). Specifically, in the 80/20 condition there would be a higher proportion of microsaccades directed toward the target throughout the cue-target interval, even during the post-inhibition rebound phase where reflexive cues typically lead to a bias away from the stimulus (Engbert & Kliegl, 2003; Hafed et al., 2021; Laubrock et al., 2005). Such sustained effects could arise from top-down control FEF's role in top-down re-orienting, which can modulate the rise-to-threshold processes of microsaccade generation to favor congruent movements (Hafed et al., 2021; Peel et al., 2016).

Thirdly, it was predicted that the functional coupling between microsaccade direction and behavioral efficiency—specifically RT facilitation—would be systematically modulated by the strategic utility of the spatial cue (Lv et al., 2022, Willett & Mayo, 2023). It was hypothesized that the link between congruent microsaccades (those directed toward the cued location) and faster response onsets would be greater in the 80/20 predictive regime than in the 50/50 non-predictive regime. Previous empirical evidence indicates that perceptual performance, including discrimination accuracy and RT, is at its peak specifically at the goal of an intended saccade

(Deubel & Schneider, 1996; Kowler et al., 1995). Therefore, congruent microsaccades occurring during the cue-target interval in a predictive block reflect a prioritized motor plan that "primes" the sensory system, resulting in significant reaction time benefits once the target appears (Hafed & Clark, 2002; Liu et al., 2022; Lowet et al., 2018). Conversely, the 50/50 non-predictive regime emphasizes the purely reflexive, bottom-up capture associated with stimulus-driven orienting (Irons et al., 2012; Olk et al., 2014). In this state of high informational entropy, the brain's internal generative model lacks the statistical regularities required to anchor a stable, sustained priority map (Fiebelkorn & Kastner, 2019; Vossel et al., 2014).

Methods

Participants

Complete eye-tracking datasets for the two studies were obtained from a total of 43 healthy undergraduate volunteers at the University of California, Davis. All participants were right-handed, had normal or corrected-to-normal vision, gave informed consent, and were either paid (\$15 per hour) or given class credit for their participation. As noted earlier, these data were gathered together with EEG data, and the EEG methods will be describe in Chapter 3 where the EEG data are analyzed together with eye-tracking data.

Experiment 1a: Twenty-one healthy right-handed human volunteers participated in this study ($M \pm SD = 19.81 \pm 2.29$ years of age, 15 females, 2 corrected-to-normal vision with contact lenses). Eleven additional volunteers were not included in the final dataset. Of these, three completed only one of the two required recording sessions, four failed to achieve the criterion accuracy in the spatial attention task, and four were excluded due to their inability to adequately follow task instructions, specifically maintaining fixation on the central dot.

Experiment 1b: Twenty-two healthy right-handed human volunteers participated in this study (19.86 ± 2.1 years of age, 18 females, 5 corrected-to-normal vision with contact lenses). Twelve additional volunteers were not included in the final dataset. Of these, three completed only one of the two required recording sessions, two failed to achieve the criterion accuracy in the spatial attention task, four were excluded due to excessive trial rejection resulting from data errors, and three were excluded due to their inability to adequately follow task instructions, specifically maintaining fixation on the central dot.

Stimuli and Experimental Paradigm

Participants were comfortably seated in an electrically-shielded, sound-attenuating room (ETS-Lindgren, USA). Their head position was fixed via a head and chin rest. Stimuli were presented on a VIEWPixx/EEG LED monitor, model VPX-VPX-2006A (VPixx Technologies Inc., Quebec Canada), at a viewing distance of 90 cm, vertically centered at eye level. The display measured 24 inches diagonally, with a native resolution of 1920 by 1080 pixels and a refresh rate of 120Hz. The recording room was dimly illuminated using DC lights.

Participants engaged in a modified Posner cueing paradigm (Posner, 1980) in which their task was to perform an orientation discrimination task (see Figure 2.1). They were instructed to focus their gaze on a small (4 minutes of arc diameter) white fixation dot (Cherici, Kuang, Poletti, & Rucci, 2012) throughout the entire experiment. At the beginning of each block, participants were instructed to attend in the direction of one of two colors of a double-sided arrow which they were told would most likely predict the side of the upcoming target. In Experiment 1a, the relationship between the cue and target side was valid on a random 80% of trials. In Experiment 1b the cue was valid on a random 50% of trials. In both experiments participants were told to respond to all targets, regardless of whether they appeared on the cues side, and thus they reoriented attention

to the opposite hemifield when the cue did not predict the target side (so-called invalid trials). In Experiment 1a, a random 20% of trials had invalid cues and in Experiment 1b, 50% had invalid cues.

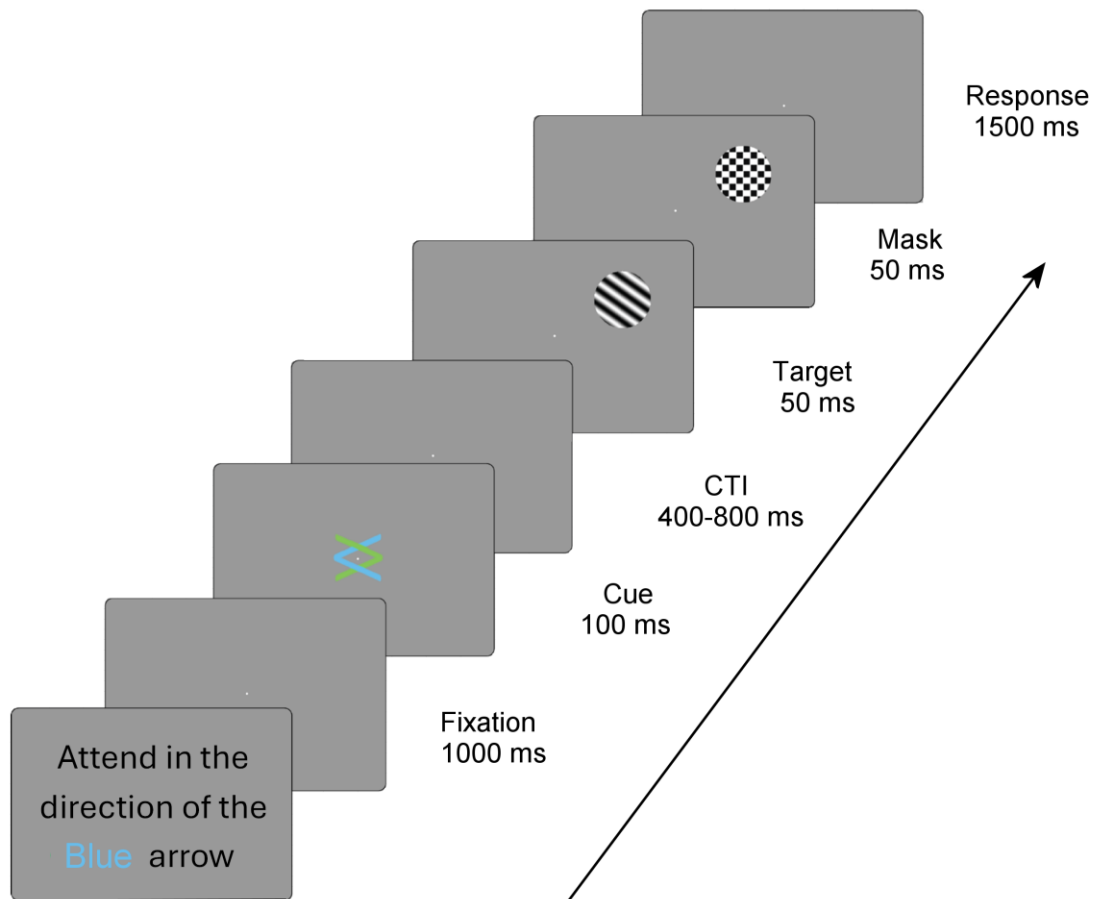


Figure 2.1. Covert spatial attention task. For each block, participants were instructed to attend in the direction of either blue or green while maintaining central fixation, and to press the left or right arrow key depending on the orientation of the lines within the target. Targets were immediately masked by a patterned stimulus.

On each trial, after a 1000 ms period to correct for small eye drifts, participants were presented with the central arrow *cue* for 100 ms and this was followed by a variable interstimulus interval (ISI) of 400-800 ms (mean 600 ms). At the end of the ISI, a square-wave grating *target* (6 cycles/degree, 2° in diameter) would appear 1° above and 4° either to the left or the right from central fixation for 50 ms. The target was immediately followed by a 50 ms checkerboard mask (6 cycles/degree). The subjects' task was to use their right hand to press the left and right arrow keys of a PC keyboard to respond to the orientation of the lines within the target square-wave grating (that is, press the left button with their index finger if the gratings tilted left, and press the right button with their middle finger if the gratings tilted right). There was a total of 500 trials in each session, and all participants came to the lab on two different days for a total of two recording sessions (1000 trials total).

Eye-Tracking Methods

Eye-tracking acquisition: During each experiment binocular eye movements were continuously monitored with an EyeLink 1000+ with a binocular sampling rate of 1000 Hz (SR Research Ltd., 2014). Participants sat 90 cm from the monitor, and head movements were minimized using a chin and forehead rest. The eye-tracker was placed 15 cm in front of the monitor and ~75 cm away from participants' eyes. Eye calibration and validation were accomplished with the built-in EyeLink protocols, and gaze position was converted from .edf format into .asc format for analysis.

Microsaccade detection and pre-processing: Microsaccade detection followed Engbert and Kliegl (2003) where eye-positions were transformed into velocities with a moving average of 6 time points. Velocity threshold for horizontal and vertical eye positions was first calculated using custom MATLAB scripts and analysis protocols from Pastukhov and Braun (2010), then

separately defined by 6 times the median-based estimator for the standard deviations of the velocity distributions. Trials larger than 1° were excluded from analysis. For each analysis (rate, amplitude, and direction), microsaccades were categorized based on whether they were made towards or away from the direction of the cue.

Microsaccade Rate: Microsaccade rate for both eye-movements made towards or away from the cue were calculated separately from 250 ms before cue onset to 800 ms after cue onset. Rate was calculated based on the saccade onset by averaging the number of microsaccade onsets per time sample across all trials in a given condition, multiplying these values by the sampling rate to convert to Hz, and subsequently smoothing over using a 100 ms simple moving average using the current time point and 99 past time points (Engbert & Kliegl 2003, Laubrock et. al, 2005, Lv et. al, 2022). Finally, microsaccade rate was baselined to zero relative to cue onset.

Microsaccade Amplitude: Microsaccade amplitude for both eye-movements made towards or away from the cue were calculated similarly as above. Microsaccade horizontal amplitude was used for this analysis, specifically using the formula $\text{Horizontal Amplitude} = \text{Microsaccade Amplitude} * \cos(\theta)$ where θ is the angle made from the microsaccade and horizontal axis (Lv et. al, 2022). Afterwards, amplitude over time was binned and smoothed using the same procedure as described above (Lv et. al, 2022; Xue et. al, 2017).

Microsaccade Direction: Because rate and amplitude analyses do not take into consideration microsaccade direction, microsaccades were split in these analyses into 3 different 150 ms time bins time-locked to cue onset. Intervals were as follows: pre-cue -150-0 ms (Interval 1), the beginning of the CTI interval 150-300 ms (Interval 2), and later CTI interval (300-450 ms) (Interval 3). In each time bin, microsaccades were further binned based on θ in radians in 30 equally spaced bins. Microsaccade direction in each time bin was quantified by the difference of

the relative frequency of congruent and incongruent microsaccades similar to Laubrock and colleagues (2005). This was calculated as the difference between the toward and away microsaccade relative frequencies for the three time bins.

Microsaccade Analysis: To analyze microsaccade rate and amplitude within each Experiment, repeated-measures ANOVAs were used with factors of time window (the three-time windows) and direction (towards or away from the cue direction) as the within-subjects factors. Follow-up ANOVAs were used when there was an interaction between Time window and direction. To analyze the time-course of the cueing effect seen in rate and amplitude within each study, the difference waves between towards and away microsaccades were put in a one-way ANOVA contrasting the respective three-time windows. The same procedure was also used for directionality, but for the three different time intervals and the difference between the relative frequencies for towards and away microsaccades in each time interval instead. These final analyses used chi-square statistics rather than ANOVAs.

Results

Experiment 1a

Behavioral Data:

Analysis of the RT data for the 80% probability study showed a main effect of Validity ($F(1,19) = 9.51, p = 0.006$), with faster RTs for valid (529 ± 75) than invalid trials (546 ± 80), but there was not a main effect of MStype for RT ($p > .65$). While the interaction between validity and MStype was not significant ($p > .36$), because a priori predictions were primarily focused on the question of validity effects in the congruent (as opposed to incongruent) condition as outlined in the Methods, we nevertheless did the planned comparisons of the validity effect for each of the MStypes. Importantly while participants responded faster for valid than invalid trials

following congruent ($F(1,19) = 10.38, p = 0.005$) and No MS events ($F(1,19) = 9.51, p = 0.006$), there was no validity effect in the incongruent MS case ($p > .98$ – see Figure 2.2). In the case of response accuracy there were no significant main effects or interactions for MSType or Validity in any of the comparisons (all $ps > .42$ see Figure 2.3).

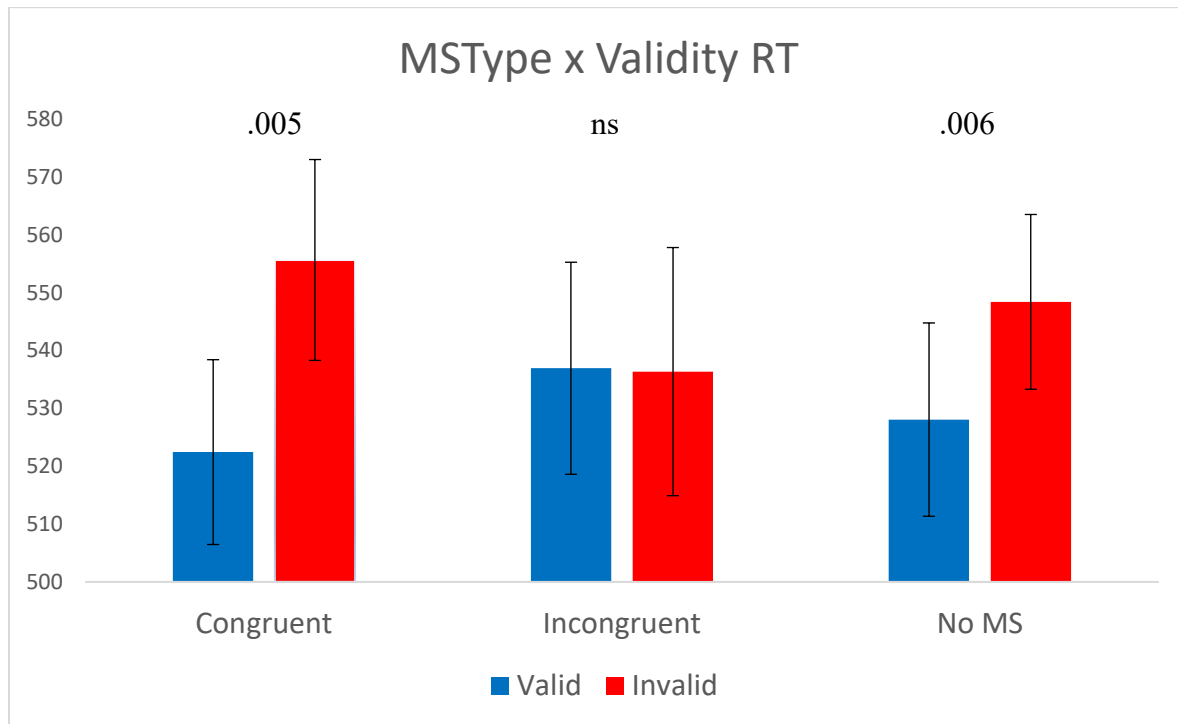


Figure 2.2. MSType x Validity RT data (time in msec on the Y-axis)

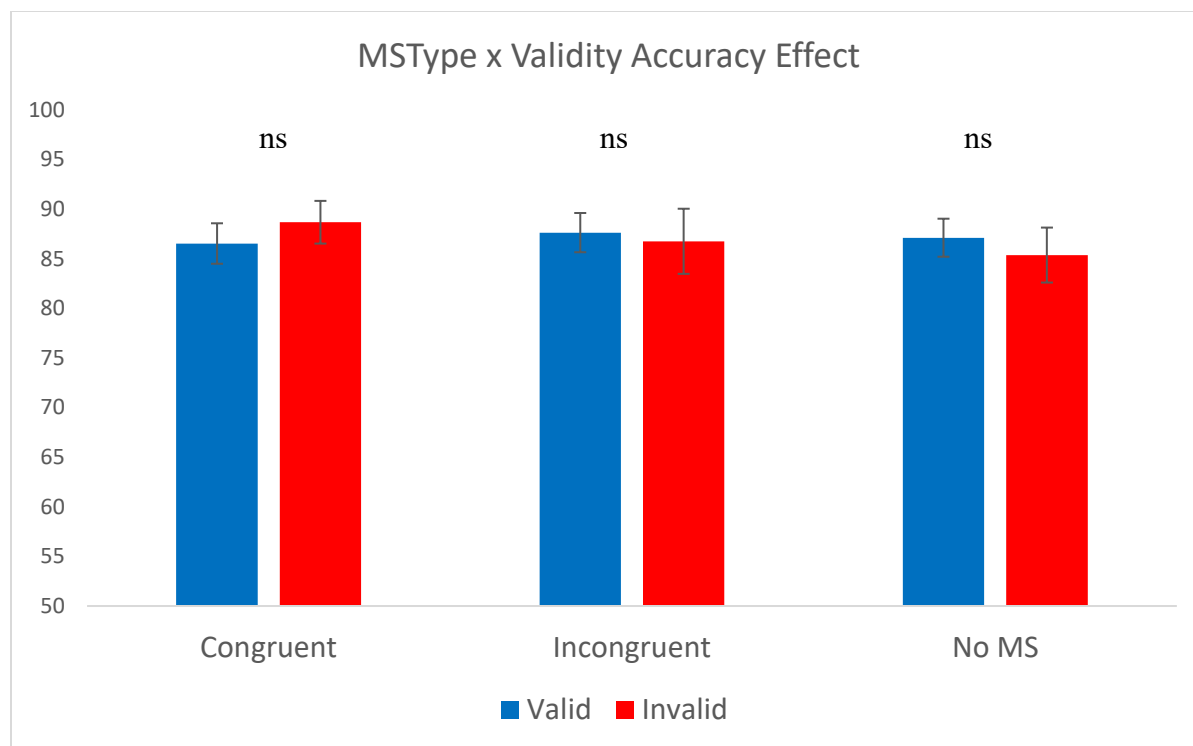


Figure 2.3. MSType x Validity Accuracy data (percent correct on the Y-axis)

Eye-Tracking

Table 2.1 shows the number of trials with at least one microsaccade per participant for each of the three MSType conditions (congruent, incongruent, no microsaccade), and Figure 2.4 shows the percentage of trials with at least one microsaccade made towards (congruent) or away (incongruent) for the two experiments. Figure 2.5 shows the overall microsaccade rate (shading denotes SEM).

Rate and amplitude

In the 80/20 experiment there was an interaction between MS Congruency and Time window of analysis for both the MS rate data ($F(2,40) = 6.57, p = .015$) and MS amplitude data ($F(2,40) = 5.14, p = 0.01$). Follow-up analyses showed that only the third window (300-450 ms) produced a significant congruency effect, and this was for both MS rate ($F(1, 20) = 7.22, p = 0.014$) and MS amplitude ($F(1, 20) = 5.52, p = 0.03$; see Figure 2.6).

Direction

As mentioned above, because rate and amplitude analyses do not take into consideration the direction of the microsaccades, in the current analysis the direction (whether the microsaccade was made towards or away from the cued direction – note since these data are based on the cue interval they are not evaluating the eventual validity) is investigated. To test this a Chi-Square test of independence was performed for each of the three time windows. For the first two time windows there were no significant differences (p 's > .7). However, for the third time-window there were significantly more microsaccades made towards (77.9 ± 50.32) compared to away (68.15 ± 46.97) from the cued direction, $\chi^2(2, N = 150) = 14.25, p = .043$ (Figure 2.6, top).

Participant	valid congruent	valid incongruent	valid no ms	invalid congruent	invalid incongruent	invalid no ms
1	145	145	228	143	144	195
2	138	93	260	138	151	220
3	48	36	422	45	31	418
4	111	82	307	99	57	344
5	214	93	204	194	83	212
6	135	119	405	92	88	161
7	82	73	371	91	59	324
8	91	48	355	93	66	347
9	65	36	699	21	6	173
10	325	336	139	79	88	33
11	395	119	286	95	23	82
12	261	242	297	64	72	64
13	426	259	115	116	58	26
14	257	233	310	76	52	72
15	479	58	263	121	13	66
16	127	112	561	20	38	142
17	124	75	601	30	24	146
18	246	182	372	63	32	105
19	277	87	436	78	23	99
20	480	215	105	110	62	28
21	183	75	542	48	20	132
Average	219.47619	129.42857	346.57143	86.47619	56.666667	161.38095

Table 2.1. Depicting the number of trials with at least one microsaccade per participant for each of the three MStype conditions (congruent, incongruent, no microsaccade) for valid and invalid trials for Experiment 1a.

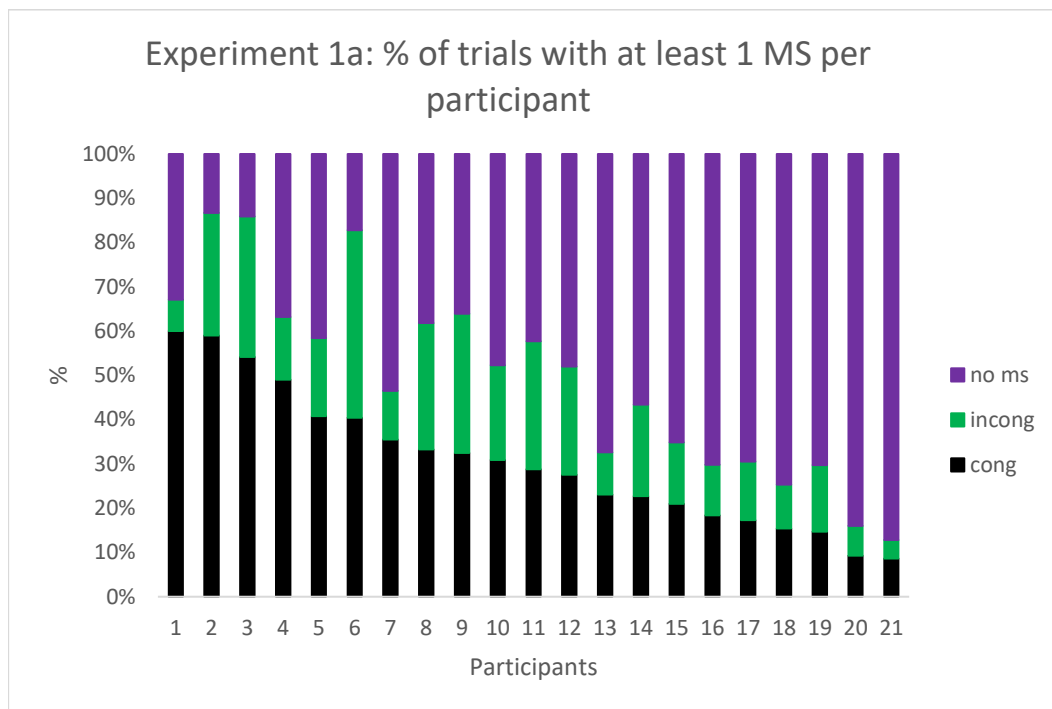


Figure 2.4. Bar graph showing the percentage of trials with at least 1 microsaccade made towards (congruent) or away (incongruent) from the upcoming target, or no microsaccade for Experiment 1a.

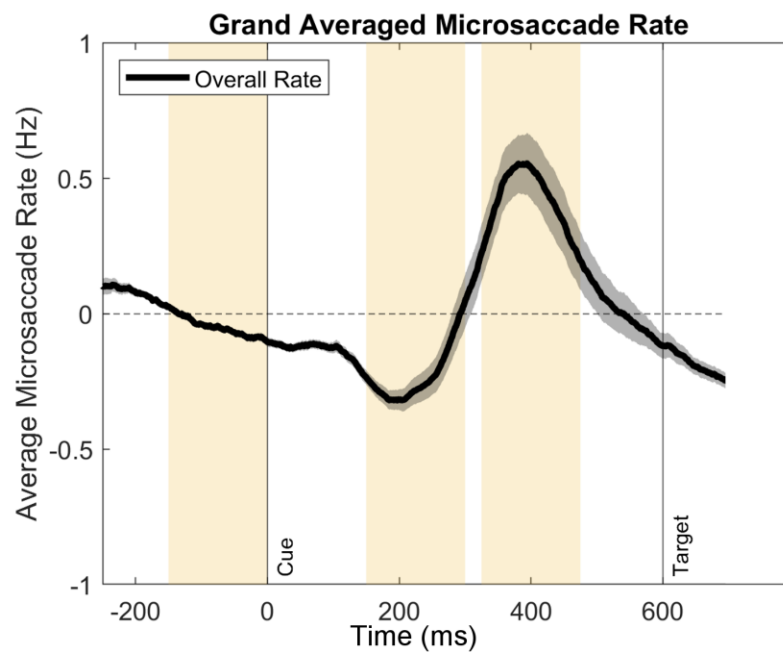


Figure 2.5. Overall rate of microsaccades for Experiment 1a (80/20).

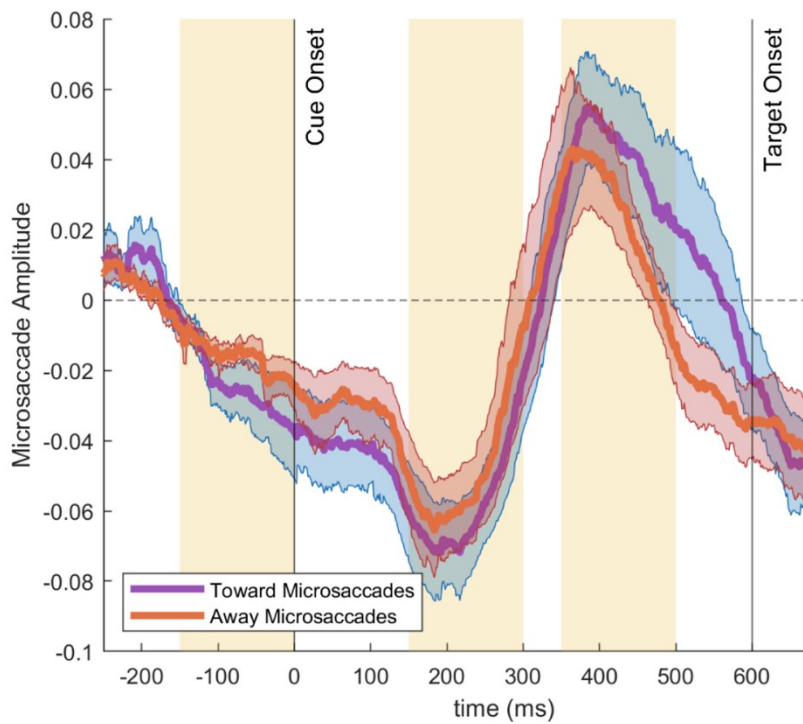
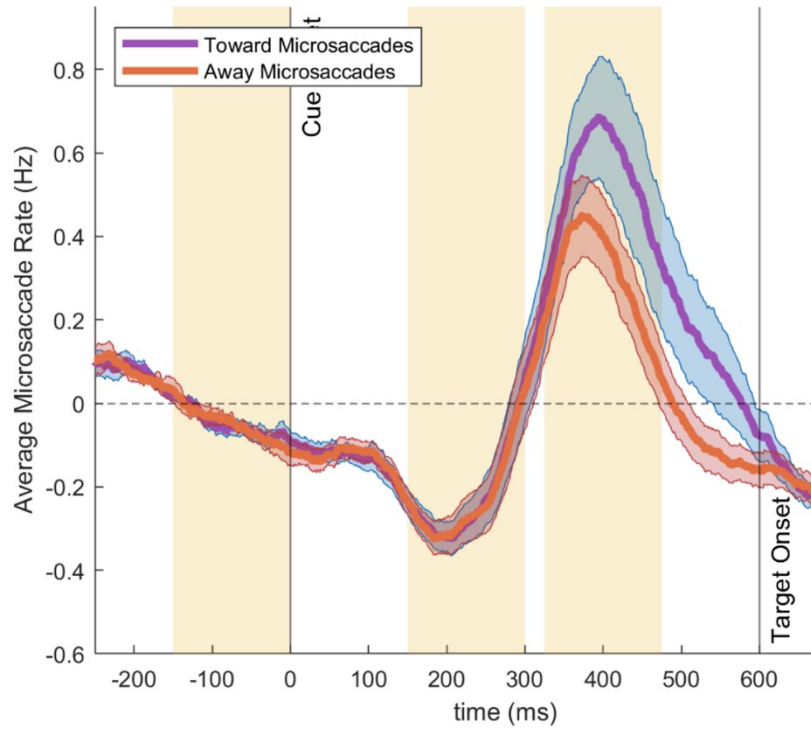


Figure 2.6. MS rate (top) data and MS amplitude (bottom) data.

Experiment 1b.

Behavioral Data:

Analysis of the target RT and accuracy data only showed a marginal effect of Validity for RT ($F(1,21) = 3.39, p = 0.08$). The analyses looking at the Validity effect separately for the three MSTypes revealed that only the No MS condition produced a significant effect ($F(1,21) = 6.25, p = 0.021$) with Valid trials producing faster responses than Invalid trials (see Figure 2.7). There were no significant effects for accuracy (all $ps > .30$ – see Figure 2.8).

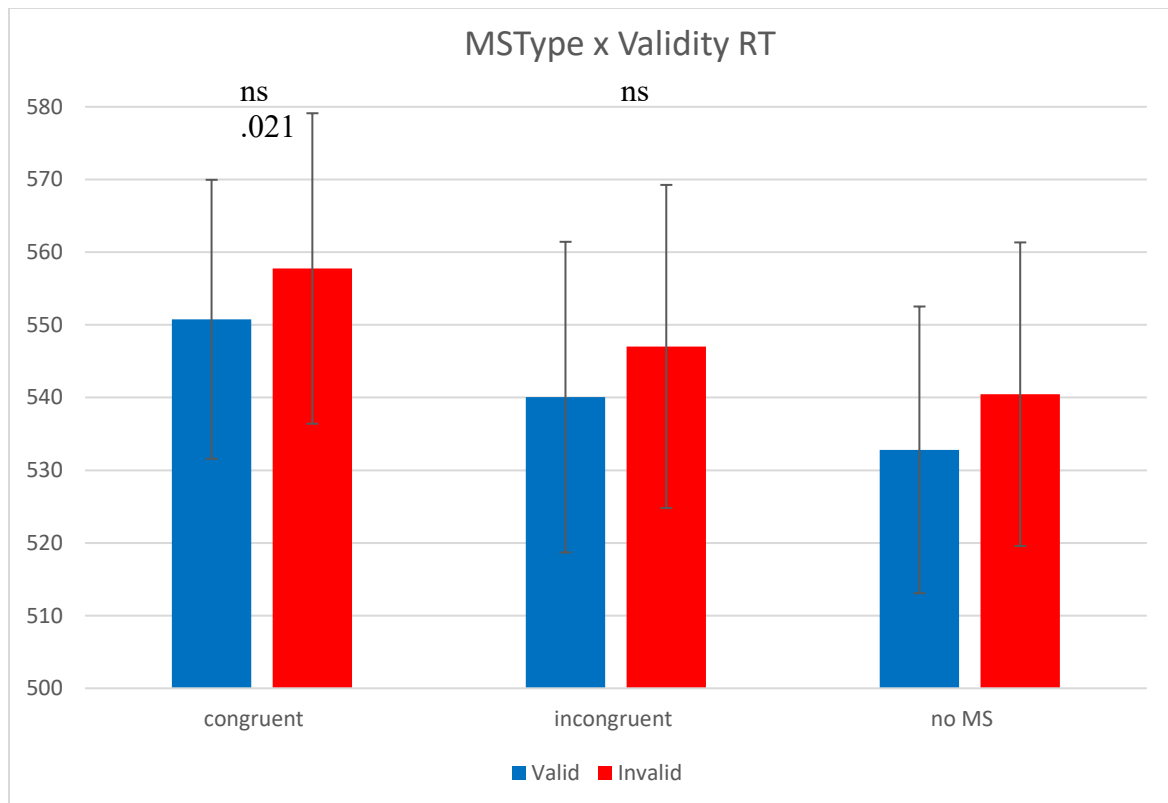


Figure 2.7. Experiment 2b (50/50) RT effects

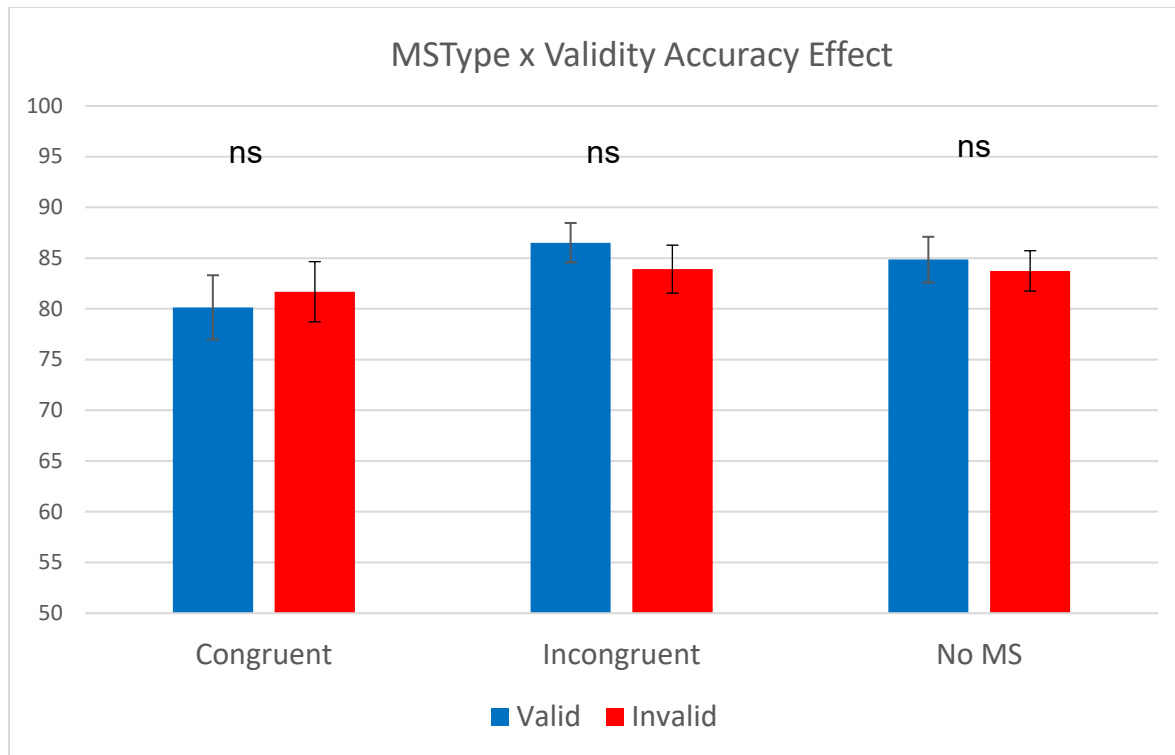


Figure 2.8. Experiment 2b (50/50) Accuracy effects

Eye-Tracking

Table 2.2 shows the number of trials with at least one microsaccade per participant for each of the three MSType conditions and Figure 2.9 shows the percentage of trials with at least one microsaccade made towards (congruent) or away (incongruent). Figure 2.10 shows the overall microsaccade rate.

Rate and amplitude

In the analysis of the MS rate and amplitude data for the 50/50 experiment there was an interaction between MS Congruency and Time window of analysis for both rate ($F(2,40) = 5.37$, $p = .031$) and amplitude ($F(2,40) = 5.41$, $p = 0.008$). Follow-up analyses showed that none of the different time windows (1, 2 or 3) showed a congruency effect for rate (although window 3 showed a trend in the right direction, $p = .15$; see Figure 2.11 top), but the third window did

show a significant amplitude effect for MS amplitude ($F(1,20) = 5.58$, $p = 0.028$; see Figure 2.11 bottom) with greater amplitude for congruent MS.

Direction

To test whether microsaccade direction systematically differed as a function of the cue (whether a microsaccade was made towards or away from the direction of the cue – as in the prior analysis in Experiment 1a, target validity is not considered here), a Chi-Square test of independence was performed for each of the three time windows. None of the time-windows differed in the number of microsaccades made towards versus away from the cued direction (Figure 2.11, top; p 's $> .08$).

Participant	valid congruent	valid incongruent	valid no ms	invalid congruent	invalid incongruent	invalid no ms
1	23	34	460	20	18	445
2	46	75	143	53	63	170
3	31	27	434	23	29	456
4	192	121	186	186	123	192
5	77	15	399	84	18	407
6	73	79	325	83	85	355
7	45	44	409	60	48	394
8	73	70	346	90	77	344
9	137	141	215	135	145	227
10	81	47	343	93	71	365
11	90	50	367	86	36	371
12	72	76	335	90	65	362
13	25	21	464	22	28	440
14	104	61	344	80	46	365
15	139	128	226	141	131	235
16	82	44	363	92	24	395
17	138	99	259	147	95	262
18	124	113	275	116	112	260
19	38	68	372	54	54	414
20	108	103	258	90	103	288
21	128	111	274	128	112	247
22	126	125	251	125	121	252
Average	88.72727	75.09091	320.3636	90.81818	72.90909	329.3636

Table 2.2. Depicting the number of trials with at least one microsaccade per participant for each of the three MStype conditions (congruent, incongruent, no microsaccade) for valid and invalid trials for Experiment 1b.

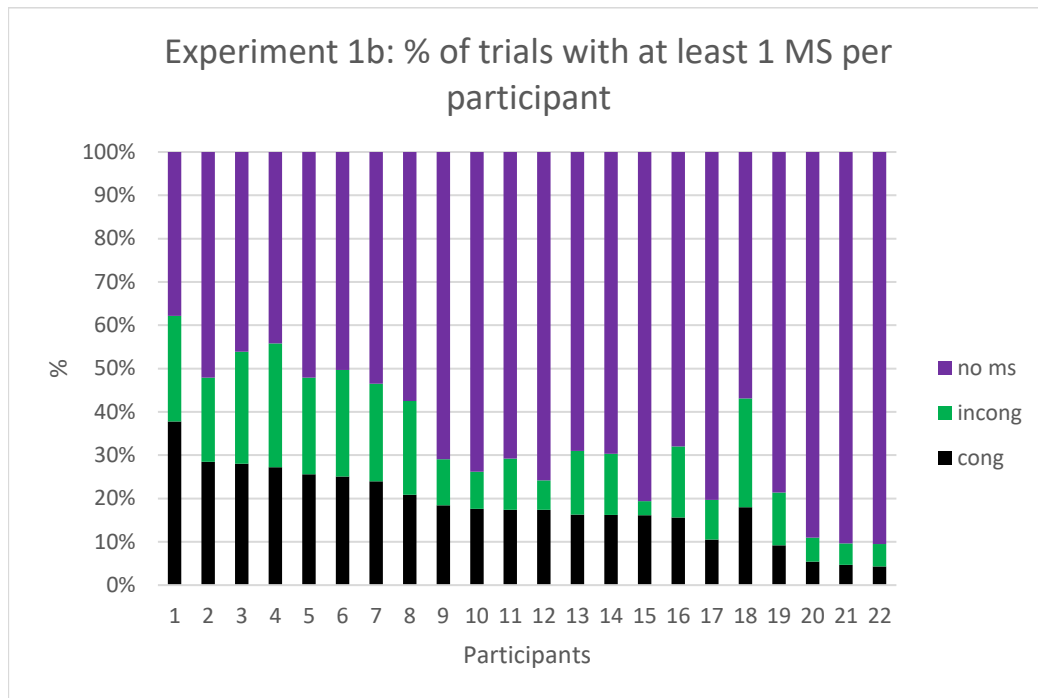


Figure 2.9. Bar graph showing the percentage of trials with at least 1 microsaccade made towards (congruent) or away (incongruent) from the upcoming target, or no microsaccade for Experiment 1b.

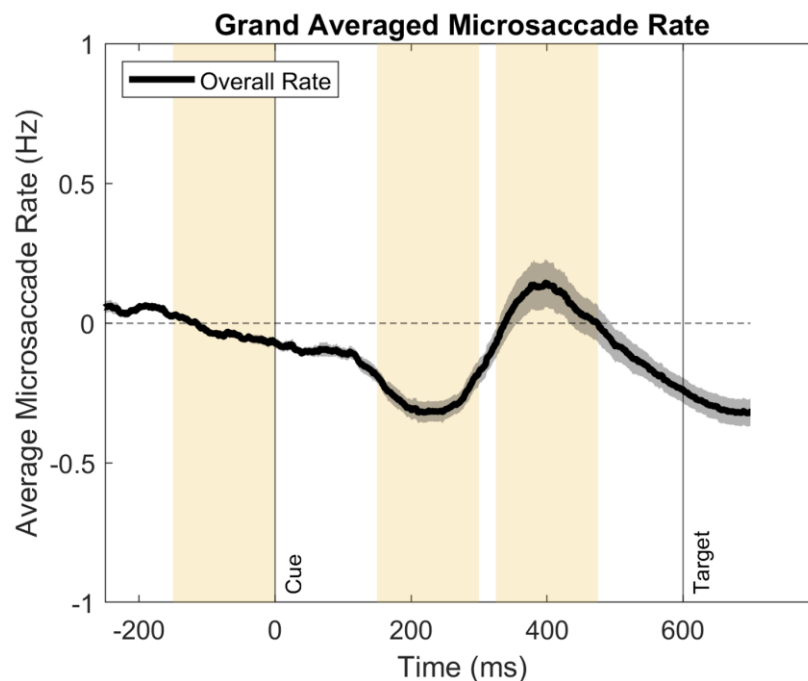


Figure 2.10. Overall rate of microsaccades for Experiment 1b

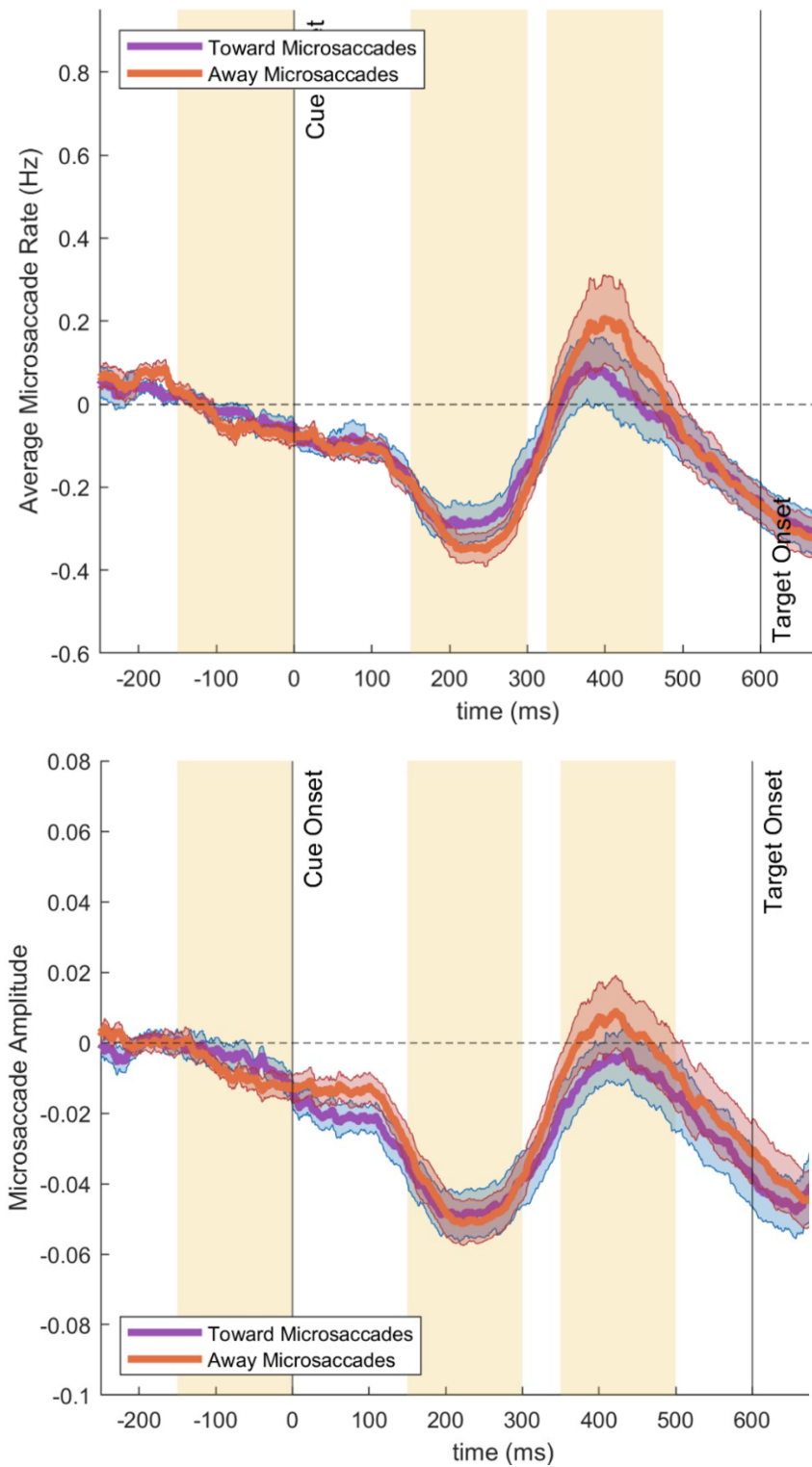


Figure 2.11. MS rate (top) data and MS amplitude (bottom) data for the 50/50 experiment across 3 epochs for congruent and incongruent MSs.

Experiment 1a and 1b comparison.

In a final analysis, the congruency MS rate effect (congruent minus incongruent) was compared in each of the three measurement windows between the two experiments. This analysis revealed an interaction of the congruency effect between Experiment and Time window ($F(2,82) = 10.99, p = .001$). This interaction is plotted in Figure 2.12 and shows a clear difference in the congruency effect for the two experiments with higher MS rates in the third measurement window in Experiment 1a where the cue validity was 80%.

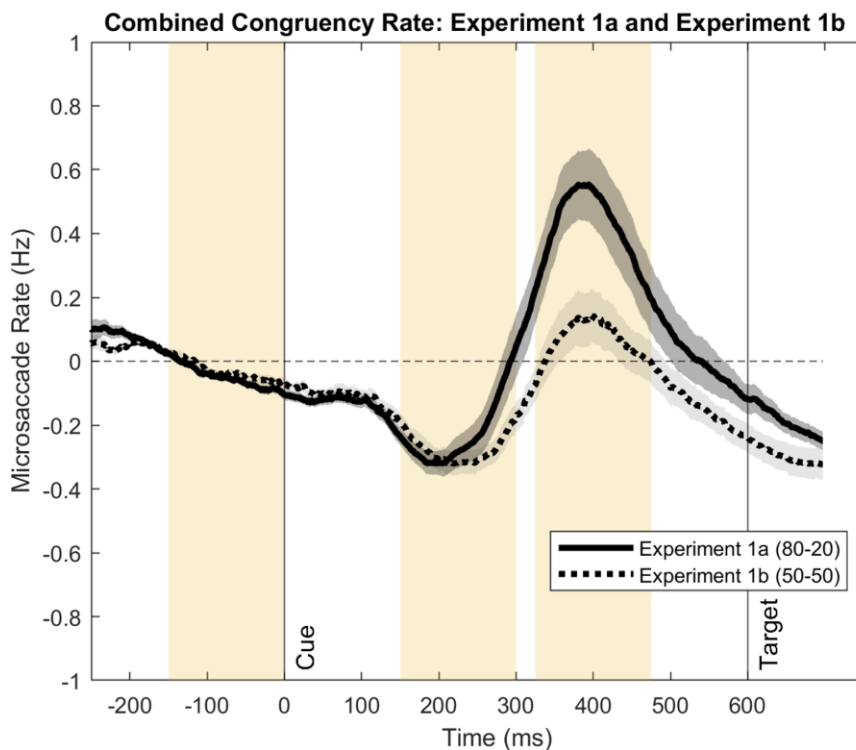


Figure 2.12. Rate plot comparing the 80/20 and 50/50 experiments

Discussion

When cues predicted target location (Exp. 1a), participants responded faster to valid than invalid targets. This was not the result of speed-accuracy tradeoffs because there was not a significant difference between the conditions in accuracy of the target discrimination, and thus provides behavioral evidence that the subjects were using the cue information. Further, when a microsaccade was made towards the subsequent target (congruent microsaccade) participants responded faster to the valid targets compared to invalid, where there was no difference. This was also true for trials on which no microsaccade was made (i.e., faster for valid).

For Experiment 1b, where cues were non-predictive (although participants were told the cues would help their performance) participants did not respond faster or more accurately to valid compared to invalid trials. Likewise, there were no microsaccade-related benefits to behavior.

Overall, microsaccades in both experiments (80/20 and 50/50 validity) followed the predicted pattern: presentation of the central cue caused an initial drop in microsaccade rate known as microsaccade inhibition starting around 100 ms after cue onset, followed by a rebound period of increased microsaccade rate (Engbert & Kliegl, 2003; Lv et al., 2022). When cues were predictive in Experiment 1a, both microsaccade rate and amplitude were greater for microsaccades made towards versus away from the cue during the rebound period, in line with the original hypotheses. In contrast, when cues were not predictive in Experiment 1b, during the rebound time window neither rate nor amplitude differed between microsaccades made towards compared to away from the cue, again as originally hypothesized. Likewise, when the cues predicted the subsequent target side (Experiment 1a), microsaccades were systematically biased towards the direction of the cue, but not when cues had no predictive value (Experiment 1b).

I will return to the theoretical implications of these as well as the results from Chapters 3 and 4 in the General Discussion in Chapter 5.

Chapter 3: Study 2

Introduction

The eye-tracking experiments in Chapter 2 established the kinematic and temporal characterization of microsaccades—further supporting the theory that they are an overt index of attention (Engbert & Kliegl, 2003; Hafed & Clark, 2002). By examining the ERPs and event-related alpha power as a function of whether a microsaccade was made towards (congruent microsaccade) or away (incongruent microsaccade) from the upcoming target, or when no microsaccade was made, the analyses in this chapter seek to determine the degree to which these microsaccadic metrics reliably map onto attention-related neural activity.

As noted previously, the EEG data was gathered together with the eye-tracking data presented in Chapter 2. However, to distinguish between the analyses presented in Chapter 2 and the present chapter, the experiments will be referred to as Experiments 2a and 2b for simplicity. Thus, Experiment 2a is the 80% cue validity dataset, and Experiment 2b is the 50% cue validity dataset. EEG recording was time-locked to both the cue and target stimuli allowing examination of both the EEG time-frequency response as well as averaged ERPs to both stimuli. Furthermore, because eye-tracking data were also collected simultaneously, both EEG and ERP responses were sorted contingent on eye movement behavior.

The experiments in this chapter bridge the eye movements recorded in Chapter 2 and brain-based measures of attention by examining the C1, the earliest visual evoked response (50–80 ms) which is thought to be largely generated in the primary visual cortex (V1; Di Russo et al.,

2002; Foxe et al., 2008, Kelly et al., 2008), and P1/N1 ERPs. As reviewed in Chapter 1, the C1 is a unique component that can be used to test theories of early selection, as its modulation by attention would indicate that top-down signals from the DAN can influence sensory processing at the very first cortical stage in a feed-forward manner (Kelly et al., 2008, Somers et al., 1999). A critical research objective investigated here is whether microsaccades act as a potentiator for this potential early stage selection (Bouhnik et al., 2025; Lowet et al., 2018, Srinivasan et al., 2025). Specifically, it is hypothesized that the C1 and P1/N1 amplitudes will be amplified on trials with a congruent microsaccade specifically when that microsaccade reflects a high-probability (80%) top-down commitment, versus when it is non-predictive (Bouhnik et al., 2025; Srinivasan et al., 2025). This effect is predicted to be opposite following an incongruent microsaccade, or when no eye movement occurs.

The degree to which these target-locked neural responses are potentiated was hypothesized to depend on the strategic utility of the spatial cue, operationalized by the contrast between 80/20 predictive and 50/50 non-predictive validity regimes (Arjona et al., 2016; Willett & Mayo, 2023). In the 80/20 condition, the high probability of target appearance at the cued location allows the internal generative model to anchor a sustained spatial priority map, presumably in frontoparietal-collicular circuitry (Arjona et al., 2016; Fecteau & Munoz, 2006; Fiebelkorn & Kastner, 2020). This endogenous control is thought to be manifested overtly in the microsaccade rate signature, where the post-stimulus rebound (200–600 ms) reflects a state of preparatory readiness (Amit et al., 2019; Denison et al., 2019). The literature suggests that attention increases baseline neural activity in structures like FEF and SC, which in turn modulate visual cortex through descending feedback projections (Ekstrom et al., 2008; Fecteau & Munoz, 2006; Kastner et al., 1999; Moore & Armstrong, 2003). Consequently, targets appearing at high-

probability locations are expected to arrive at a "primed" visual cortex, which could result in an amplified C1 response compared to targets preceded by non-predictive cues that isolate purely reflexive, transient capture (Kelly et al., 2008; Wolf et al., 2022).

The hypothesis that cue predictiveness (80% vs. 50%) would modulate the magnitude and maintenance of the preparatory attentional set was partially predicated on the neurophysiological characterization of 8–12 Hz alpha-band oscillations as a canonical signature of human spatial cognition (Foster & Awh, 2019; Foxe & Snyder, 2011; Jensen & Mazaheri, 2010; Klimesch, 2012; Liu et al., 2024). Within this framework, contralateral event-related alpha power serves as an overt measure of gating by inhibition, where alpha power is suppressed in posterior electrodes contralateral to the attended location—reflecting increased cortical excitability—and enhanced in the ipsilateral hemisphere to suppress task-irrelevant information (Foster & Awh, 2019; Foxe & Snyder, 2011; Jensen & Mazaheri, 2010; Klimesch, 2012; Liu et al., 2024). This oscillatory lateralization is not a passive sensory response but is actively generated and maintained by top-down modulatory signals originating in the DAN, specifically involving the FEF (Capotosto et al., 2009; Corbetta & Shulman, 2002; Kastner et al., 1999; Sauseng et al., 2011). The FEF, in particular, functions as a cortical source of modulatory signals that are fed back to sensory areas like V4 to enhance neural representations (Armstrong et al., 2006; Gregoriou et al., 2012; Moore & Armstrong, 2003) and is thus a prime candidate for a system responsible for this proposed microsaccade-attention.

It is also possible, given the majority view reviewed in Chapter 1, that the C1 component may not reflect microsaccade-related effects of attention. Instead, later components such as the P1 and N1, which have been reliably shown to be sensitive to covert spatial attention manipulations (Mangun, 1995; Mangun & Hillyard, 1991), may be more likely to reveal

differences associated with microsaccade dynamics (Srinivasan et al., 2025). Thus, a second set of hypotheses was that microsaccades towards the cued target location would modulate P1 and/or N1 amplitudes as a function of target validity. More specifically, that direct examination of attention effects on the P1 and/or N1 would be most prevalent when a preceding MS was congruent with the direction of the upcoming target. Importantly, any such cueing differences should only occur in Experiment 2a where the cues are predictive, and thus generate top-down control.

Methods

Participants

Complete EEG datasets were recorded from a total of 42 healthy undergraduate volunteers at the University of California, Davis. All participants were right-handed, had normal or corrected-to-normal vision, gave informed consent, and were either paid (\$15 per hour) or given class credit for their participation. All but 3 of the current participants were the same as those used in the previous chapter.

Experiment 2a: Twenty healthy right-handed human volunteers participated in this study (19.5 ± 1.76 years of age, 14 females, 6 males, three with corrected-to-normal vision with contact lenses). A total of eleven additional volunteers were not included in the final dataset: three completed only one of the two required recording sessions, four failed to reach the criterion accuracy in the spatial attention task, and four were excluded due to inadequate compliance with task instructions, specifically failure to maintain fixation on the central dot.

Experiment 2b: Twenty-two healthy right-handed human volunteers participated in this study (19.86 ± 2.1 years of age, 18 females, five corrected-to-normal vision with contact lenses).

A total of twelve additional volunteers were not included in the final dataset: three completed only one of the two required recording sessions, two failed to reach the criterion accuracy in the spatial attention task, four had excessive EEG artefact or data errors resulting in substantial trial rejection, and three were excluded due to inadequate compliance with task instructions, specifically failure to maintain fixation on the central dot.

Stimuli and Experimental Paradigm

The stimuli and experimental paradigm were identical to those for Study 1; please refer to the Chapter 2 Methods section for the detailed descriptions of stimuli and task.

Eye-Tracking Methods

Eye-tracking methods were identical to those for Study 1. Please see the Chapter 2 Methods section for the detailed description of the eye-tracking approach.

EEG Methods

Raw EEG data were acquired with a 64-channel Brain Products actiCAP active electrode system (Brain Products GmbH) and digitized using a Neuroscan SynAmps2 input board and amplifier (Compumedics USA, Inc.). Signals were recorded with the Neuroscan Curry software (Compumedics USA, Inc.) at a sampling rate of 500 Hz and a DC to 200 Hz online bandpass. Sixty-four Ag/AgCl active electrodes in an elastic cap arranged according to the international 10-10 system (Jurcak et al., 2007) and included channel FPz and FCz assigned as ground and online reference respectively see (Figure 3.1 for the exact montage). Additionally, electrodes at sites TP9 and TP10 were placed directly on the left and right mastoids, respectively. High viscosity electrolyte gel was used at each electrode site to facilitate conduction between electrode and scalp, and impedance values were kept below 25 k Ω . Curry software was used to

record continuous EEG data and was saved into individual files corresponding to EEG recording session. Offline, all EEG data were re-referenced to the average of the two mastoids.

EEG preprocessing: EEG data preprocessing procedures were completed with the EEGLAB/ERPLab (Delorme & Makeig, 2004) and FieldTrip (Oostenveld, Fries, Maris & Schoffelen, 2011) MATLAB toolboxes. For each participant, all EEG data files imported into EEGLab and were merged into a single dataset before data processing. Each dataset was visually inspected for the presence of bad channels, and when necessary bad channels were replaced by interpolation using the EEGLab algorithm. Data were visually inspected to flag and reject trials with muscle and eye movement artifacts that occurred during cue and target presentation. Independent component analysis (ICA) decomposition was then used to remove artifacts associated with blinks.

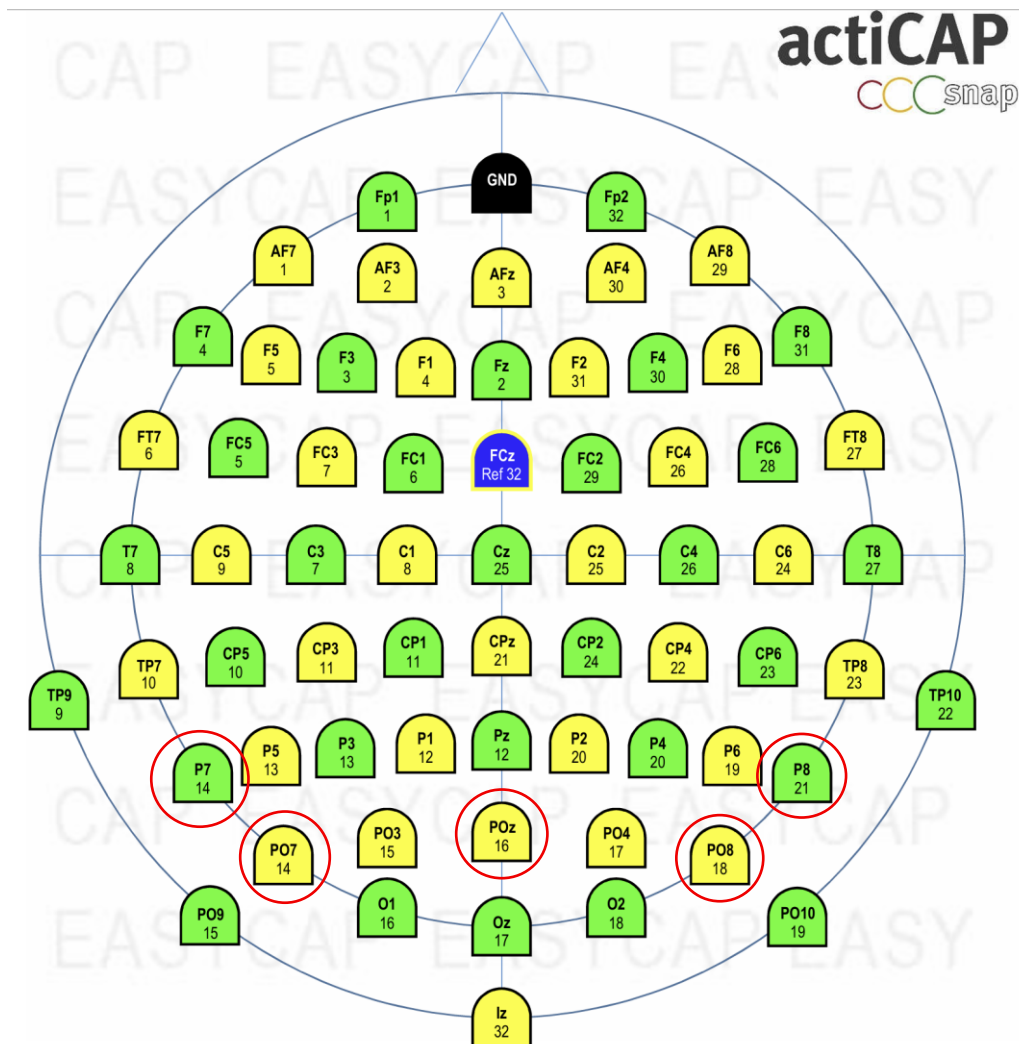


Figure 3.1. Electrode map for EEG acquisition (analysis sites circled in red).

Trial-by-trial alpha oscillation changes were extracted, aligned separately with the onset of the cues and targets using FieldTrip (Oostenveld et al., 2011). For each epoch, we computed time-frequency representations using Fourier transformation with a multi-taper sliding Hanning wavelet, adapting its length to 3 cycles for each frequency within the alpha range (8-12 Hz), at a step size of 20 ms. For each of the 42 participants, alpha power at each time point following stimulus onset was baseline corrected using a pre-cue window of -500 ms to -0 ms. Finally, we calculated the average power of oscillations across the alpha frequency range (8-12 Hz).

For ERP analysis, ERPLab was used to epoch the single trial data starting 500 ms pre-cue onset and continuing until 1500 ms post target onset. Activity in the 200 ms pre-target onset period was used as a baseline. Trials with incorrect behavioral responses or RTs that were too slow or fast (shorter than 200 ms and longer than 1000 ms) were removed prior to averaging. Averaging of the cue-locked data included bins for left direction cues and right direction cues. Target locked trials were averaged into twelve critical bins according to the factorial Posner cueing design: 2 levels of Validity (valid vs. invalid) x 2 levels of Target side (left visual field vs. right visual field) and 3 Microsaccade Types (congruent vs. incongruent vs. no MS).

EEG/ERP Analysis: In order to keep the number of factors manageable for analysis purposes while balancing the need to accurately capture the pattern of effects in the data, the number of analyzed scalp sites was limited to sites (P7/8 and PO7/8) that are near brain regions known to be sensitive to spatial attention effects on the P1 and N1 components (Mangun, 1995; Mangun & Hillyard, 1991). For the C1 component the midline site POz was used (Slotnick, 2018b). In order to understand the time course of processing, separate GLM repeated-measures ANOVAs were performed on mean amplitudes (in microvolts) in the following time epochs: 40-80 ms for the C1 measured at POz; 80 to 120 ms for the P1 component measured at P7/8 and

PO7/8; and 140-200 ms for the N1 measured at P7/8 and PO7/8. For the P1 and N1 statistical comparisons, the primary focus was on validity effects at electrode sites contralateral to the visual field of target presentation (P7/PO7 for RVF targets and P8/PO8 for LVF targets). An initial omnibus ANOVA included factors of Validity (valid vs. invalid) and MStype (congruent vs. incongruent vs no MS) and electrode (PO7/8 and P7/8). Because of the hypothesized differences in the Validity effect as a function of MStype, three separate follow-up *pre-hoc* ANOVAs examined contralateral Validity effects (Valid vs. Invalid) separately for each MStype. These analyses were the primary focus of these two experiments. Finally, to compare the results from the two experiments, a final set of ANOVAs compared validity effects (i.e., the difference in amplitude between valid and invalid trials) for the three MStypes as a function of Experiment (2a vs. 2b).

Results

Experiment 2a - 80/20 Targets

ERPs to targets:

Plotted in Figures 3.2 and 3.3 are the valid versus invalid ERPs to target stimuli at 15 representative scalp sites for left (3.2) and right (3.3) visual field stimuli. Figure 3.4 replots a subset of the data to focus on contralateral sites P7/8 and PO7/8 contralateral to the side of stimulus presentation where the P1 and N1 attention effects are typically maximal; these are also the sites used for statistical comparisons. As can be seen in all three figures, there is clear evidence of the classic early visual ERP components including the P1 and N1. Close examination of the POz site (where C1 is typically largest; Slotnick, 2018b) suggests the presence of an even earlier C1 component (Figure 3.5). Note: More fine-grained comparison plots showing ERPs in the twelve critical bins are included in the Appendix.

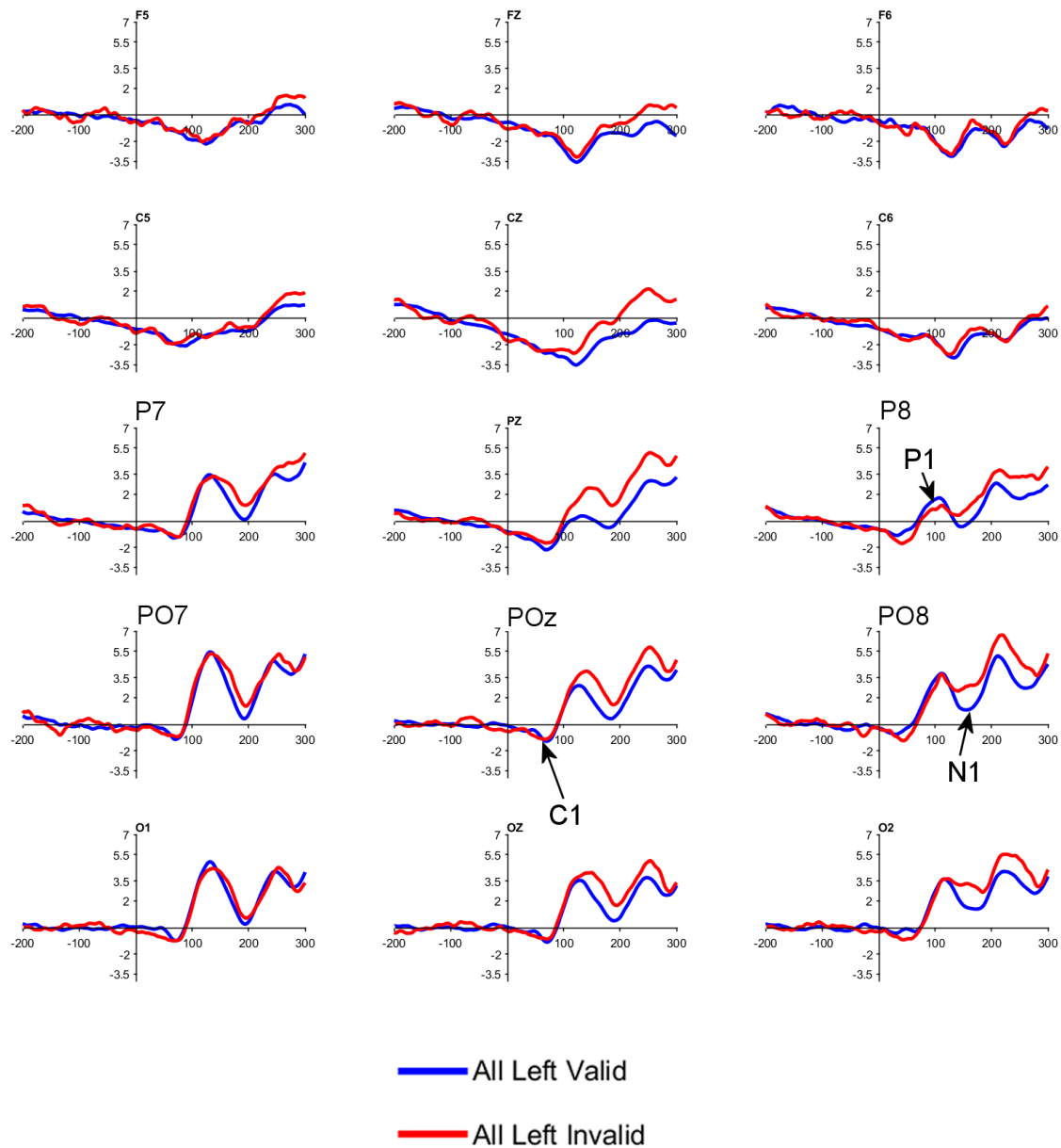


Figure 3.2. ERPs at 15 scalp sites in the 80/20 experiment for Left VF Targets in the valid (blue) and invalid (red) conditions. In this and all following figures positive is plotted up. Note the labels for the five electrode sites used in analysis are printed in a larger font.

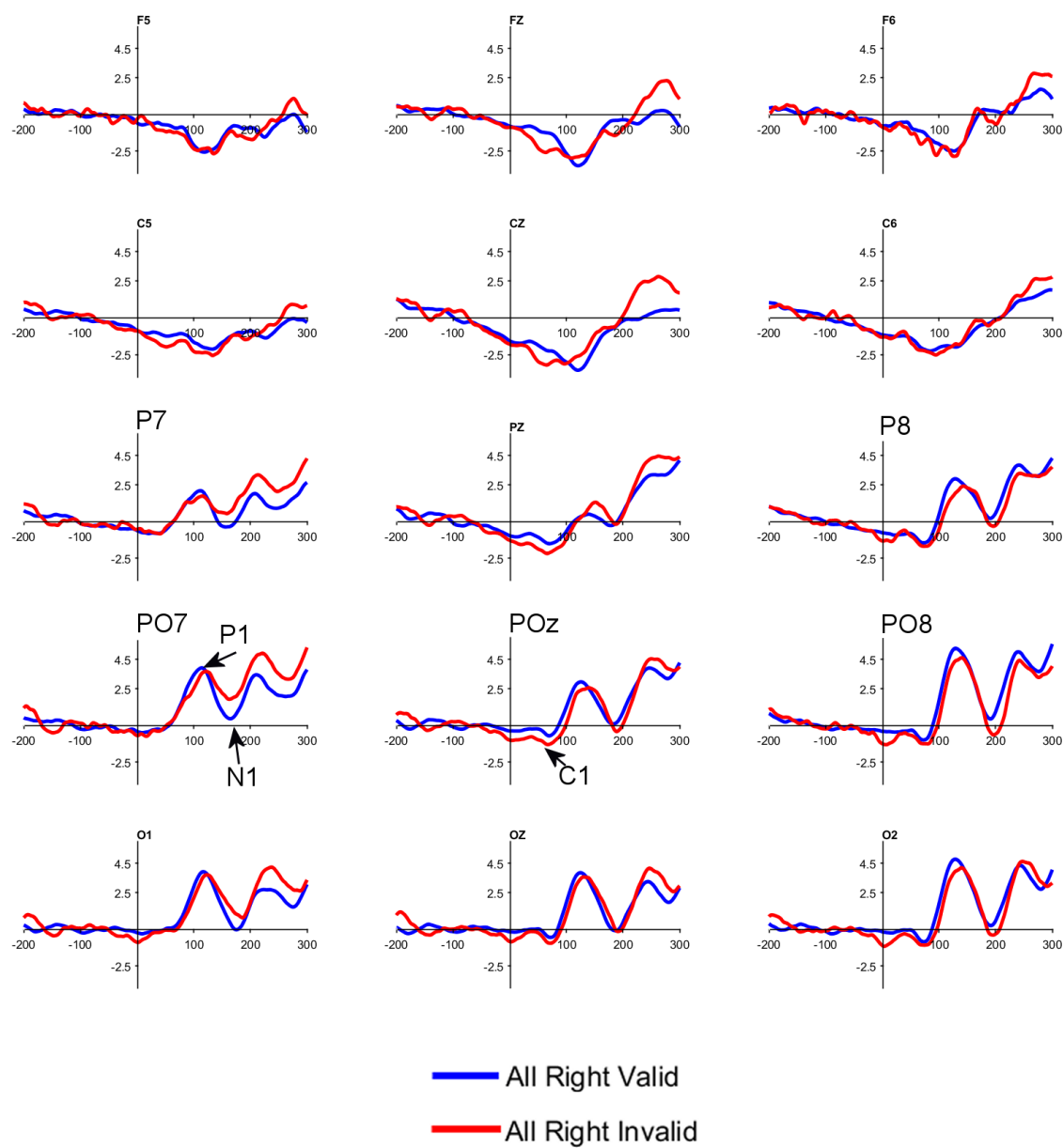


Figure 3.3. ERPs at 15 scalp sites in the 80/20 experiment for right VF Targets.

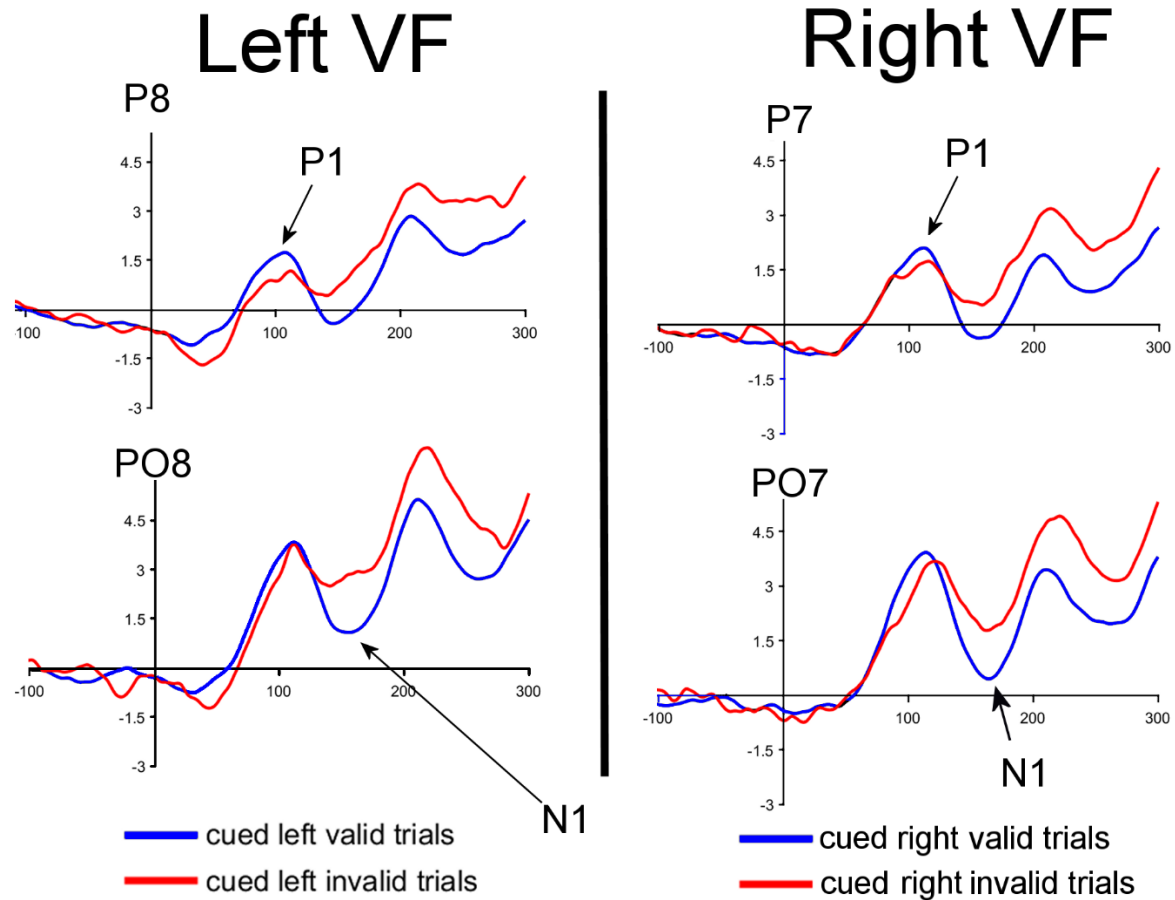


Figure 3.4. ERPs (-100 to 300 ms) for left and right VF targets contrasting the Valid and Invalid conditions at electrode sites contralateral to the side of target presentation.

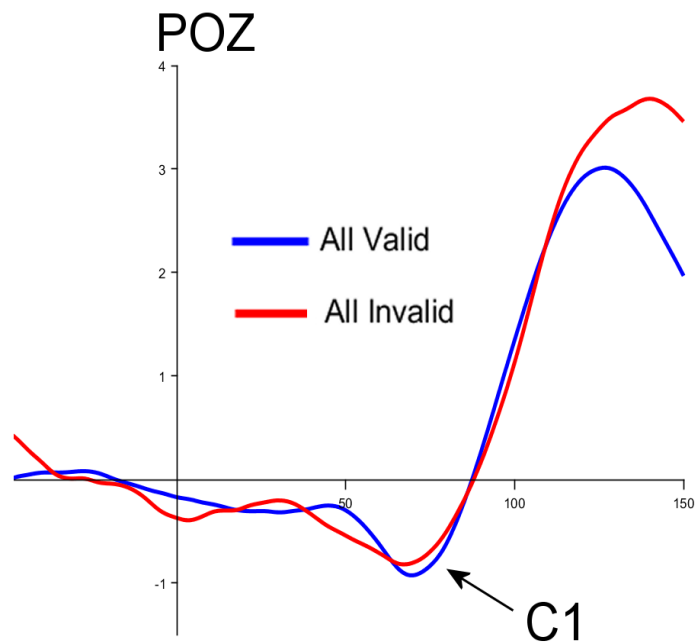


Figure 3.5. C1 at the POz site for all valid vs. all invalid targets.

C1 amplitude (40-80 ms)

There were no significant validity effects (main or interactions) on the C1 (all p s > .14 -- see Figure 3.5). The planned follow-up analyses examining the Validity effect for the three MSTypes separately also did not reveal any significant effects of Validity (all p s > .13).¹

P1 amplitude (80-120 ms)

In the P1 epoch in the omnibus ANOVA, there was a marginal contralateral main effect of Validity ($F(1,19) = 4.18$, $p = 0.055$). As can be seen in Figure 3.4 valid targets tended to have a slightly larger P1 than invalid targets at the two electrodes contralateral to the target presentation side. While the interaction between validity and MSType was not significant ($p = .51$), because our a priori predictions were primarily focused on the question of validity effects in the congruent (as opposed to incongruent) condition as outlined in the Methods, we nevertheless did the planned comparisons of the validity effect for each of the MSTypes. Planned comparisons to examine the contralateral validity effect for each of the MSTypes revealed a significant PI validity effect only for congruent trials (congruent: $F(1,19) = 5.71$, $p = 0.027$; incongruent and no MS p s > .34). This pattern can be seen in Figures 3.6 and 3.7 (and the difference waves in Figure 3.8); for congruent trials, the P1 validity difference can be observed only for the congruent microsaccade condition.

¹Note in Figures 3.6 and 3.7 that there does seem to be a notable negativity to left-sided targets at the contralateral P8 and PO8 electrodes for invalid compared to valid trials. However, exploratory analyses suggest these are not significant (all p 's > .15). Also note in Table 2.1 (Chapter 2) that there are fewer trials in the invalid incongruent condition, which suggest that this could be due to noise.

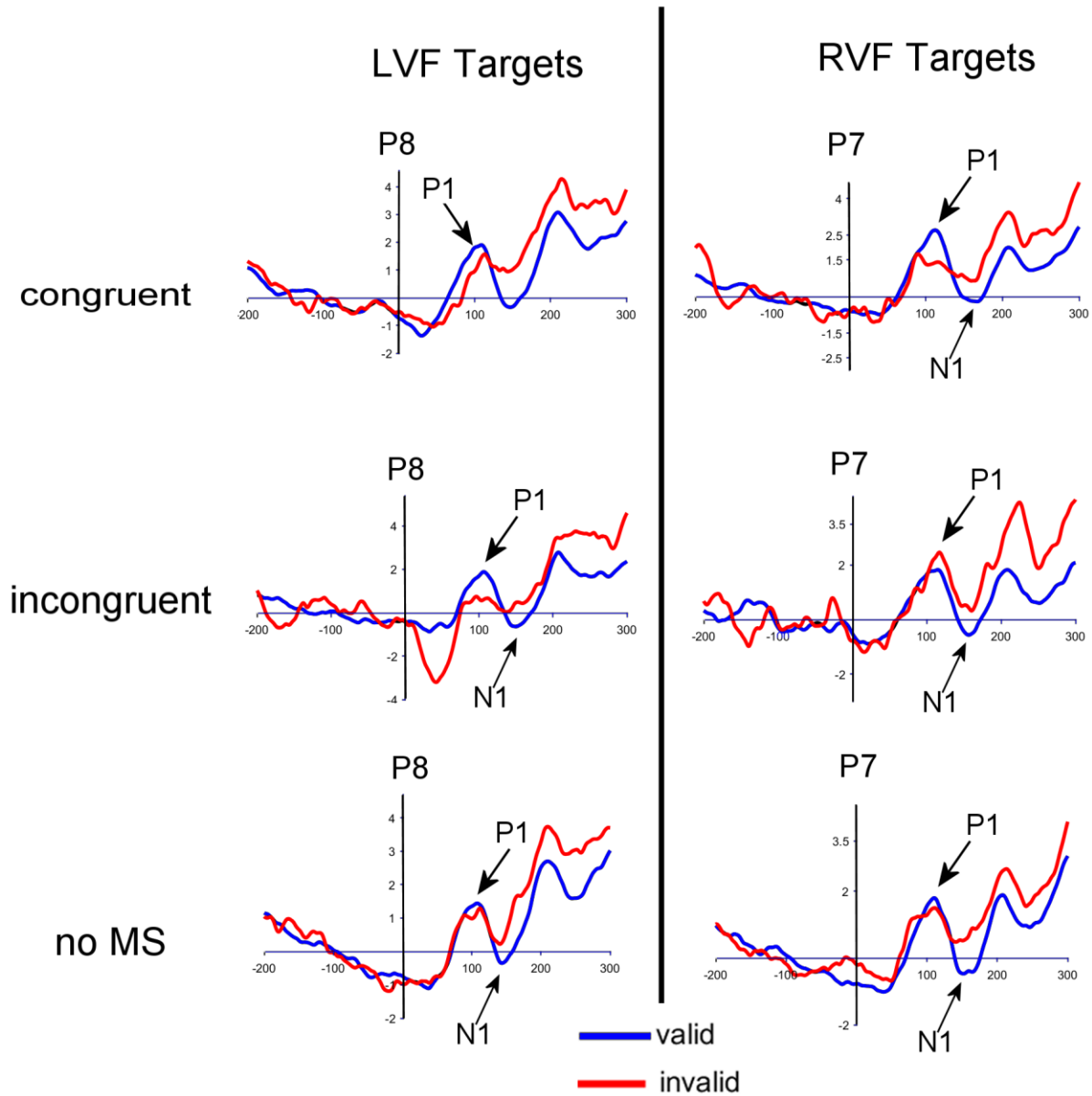


Figure 3.6. MStype x Validity x Target side at the P7/8 sites. Note the contralateral P1 attention effects for congruent but not incongruent or no MS conditions.

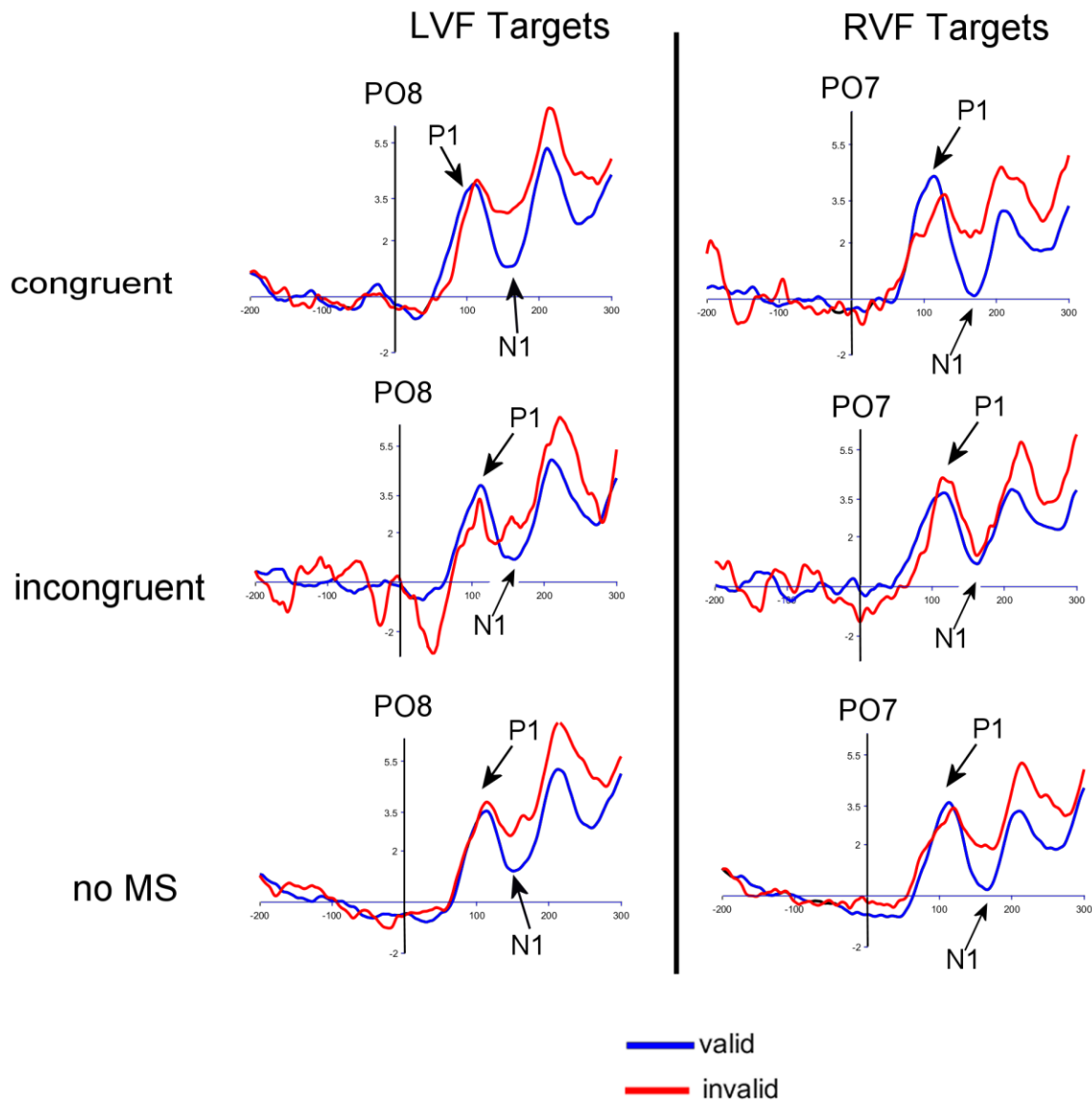


Figure 3.7. MStype x Validity x Target side x Electrode (PO7/8). Note the contralateral P1 attention effects for congruent MSs.

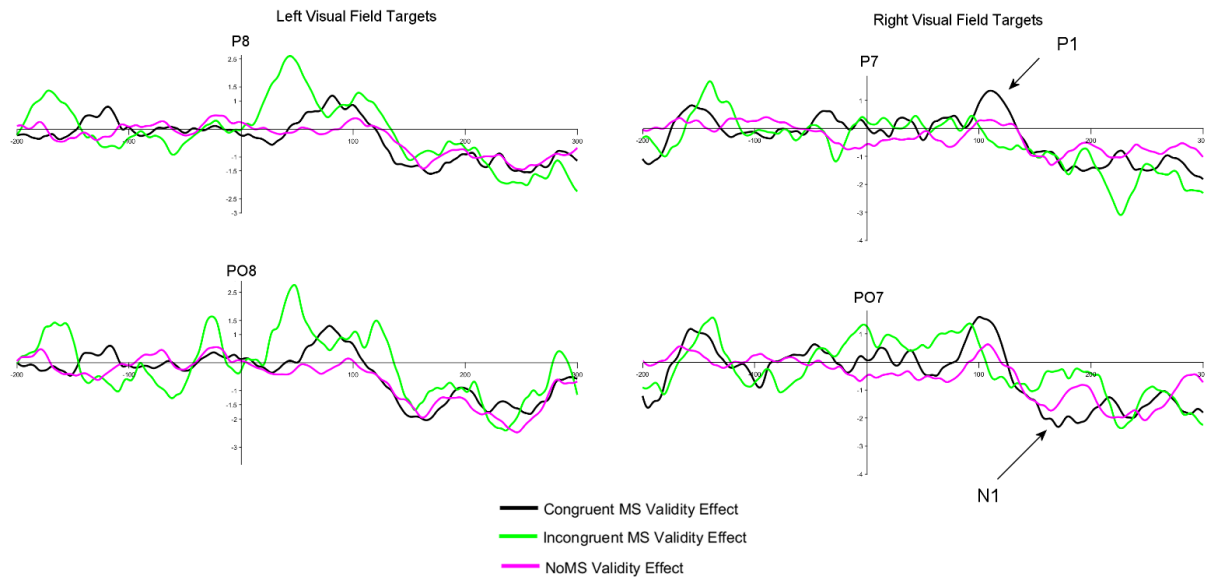


Figure 3.8. Contralateral Validity difference waves at the P7/8 and PO7/8 sites as a function target side for each of the three MSTypes (note this figure shows the same effect as Figures 3.8 and 3.9)

N1 amplitude (140-200 ms)

There was a main effect of validity for contralateral targets in this epoch ($F(1,19) = 8.73$, $p = 0.008$). As can be seen in Figure 3.4, like the P1 valid targets, contralateral to electrode location produced larger N1s than invalid targets at that same location. This effect did not differ as a function of target field (Target location $\times$ Validity interaction $p > .73$). While the interaction between validity and MSType was not significant ($p = .62$), because our a priori predictions were primarily focused on the question of validity effects in the congruent (as opposed to incongruent) condition as outlined in the Methods, we nevertheless did the planned comparisons of the validity effect for each of the MSTypes. For congruent MSs there was a significant contralateral validity effect ($F(1,19) = 12.2$, $p = 0.002$ – see Figures 3.6, 3.7 and the difference waves in Figure 3.8). For the incongruent condition there was no evidence of a validity effect ($p > .23$),

but unlike for the P1 epoch, there was a significant validity effect for the no MS condition ($F(1,19) = 9.12, p = 0.007$).

Target Alpha Power Percent Change:

In this analysis the mean percent change in alpha power between 300 and 500 ms time locked to target onset was calculated. Like the mean amplitudes from ERP data, the analysis examined validity effects at electrode sites contralateral to side of the target stimulus separately for each MStype condition. While there was no significant Validity x MStype interaction ($p = .38$), planned comparisons were nonetheless investigated. There was a main effect of Validity on percent change alpha power ($F(1,19) = 13.94, p = 0.001$) with valid trials having greater contralateral desynchronization than invalid trials (-11.92% vs. 4.9%). There was also a significant contralateral validity effect following congruent MS ($F(1,19) = 11.53, p = 0.003$ – see Figure 3.9). This same comparison did not result in significant differences for the incongruent and no MS conditions ($ps > .3$ – see Figure 3.9). The effect for congruent MSs was due to a greater decrease in alpha power (i.e., greater alpha desynchronization) for electrodes contralateral to the target when comparing valid and invalidly cued targets.

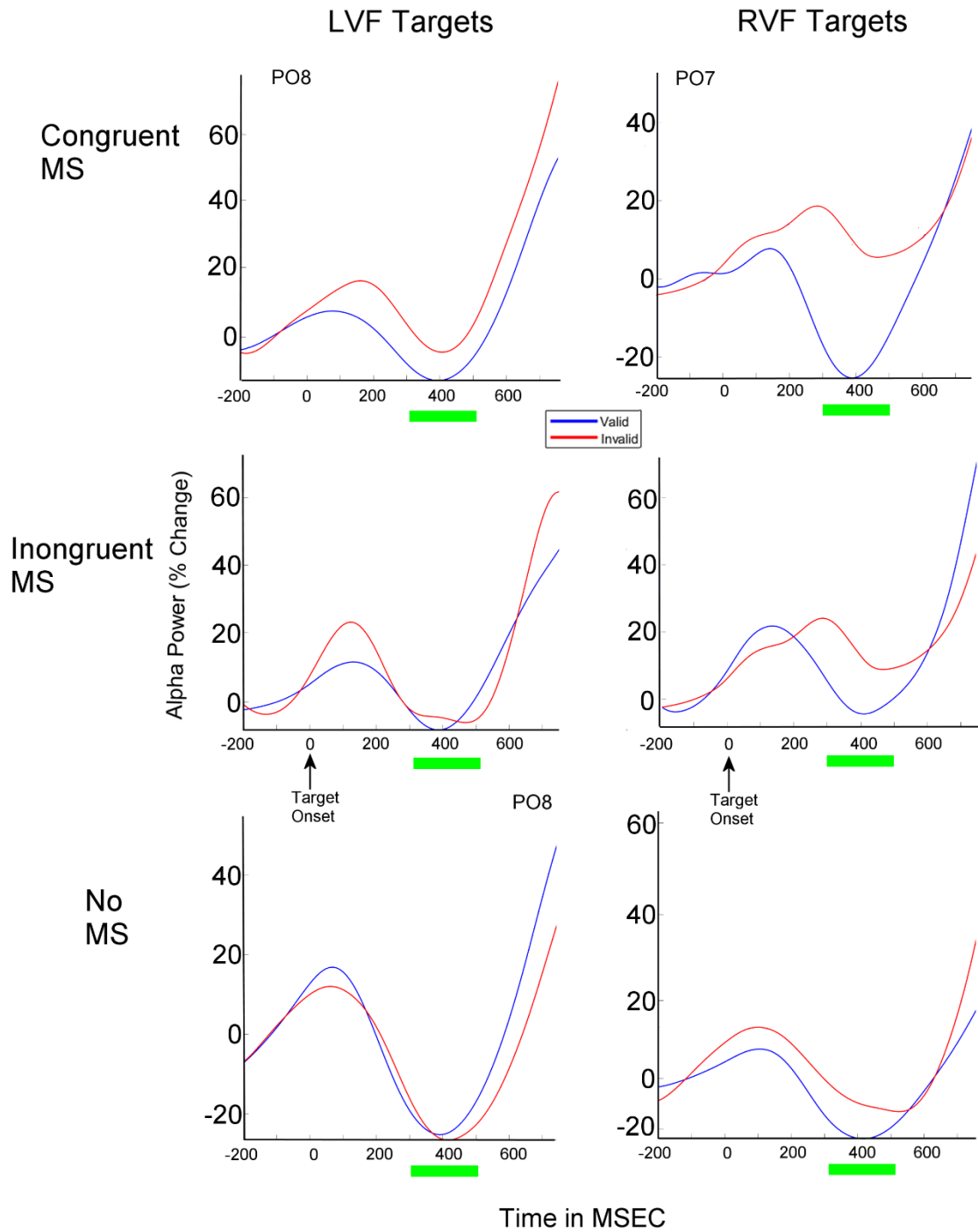


Figure 3.9. Target Alpha Power Percent change for the contralateral validity effect for each of the three MSTypes. Time window of analysis highlighted in green.

Cue-locked Alpha Power Percent Change:

Plotted in Figure 3.10 are the time course functions of alpha power percent change for left (blue) compared to right (red) cues at four electrode sites. Plotted in Figure 3.11 across several time epochs are the alpha power change scalp maps computed from the difference between the left and right cues. The analysis of these data produced a significant interaction between the Cue side and Electrode factors in 600 to 800 ms epoch following the onset of the cue (600-800: $F(1,19) = 9.68$, $p = .006$ – see Figure 3.10). This effect was due to greater alpha band desynchronization at sites contralateral to the direction indicated by the cue.

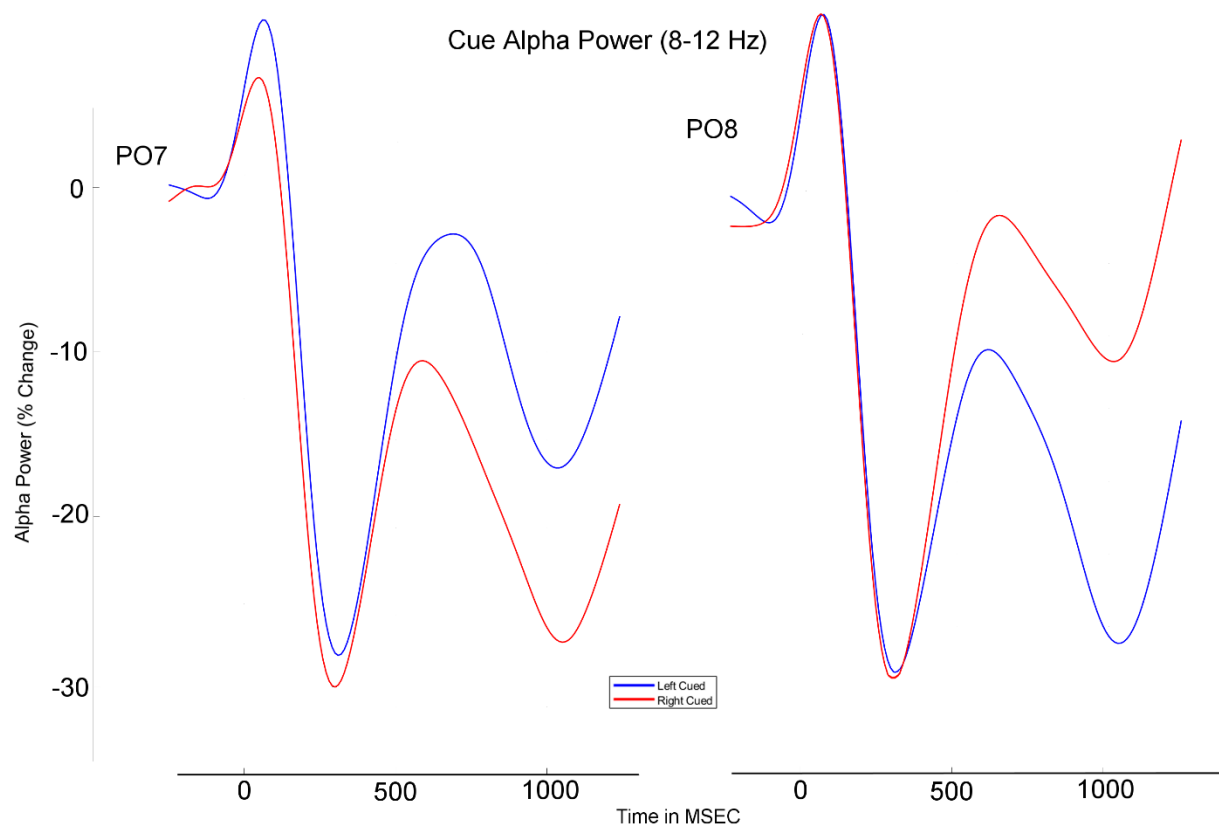


Figure 3.10. Time course of alpha power percent change to left and right cues at PO7/8.

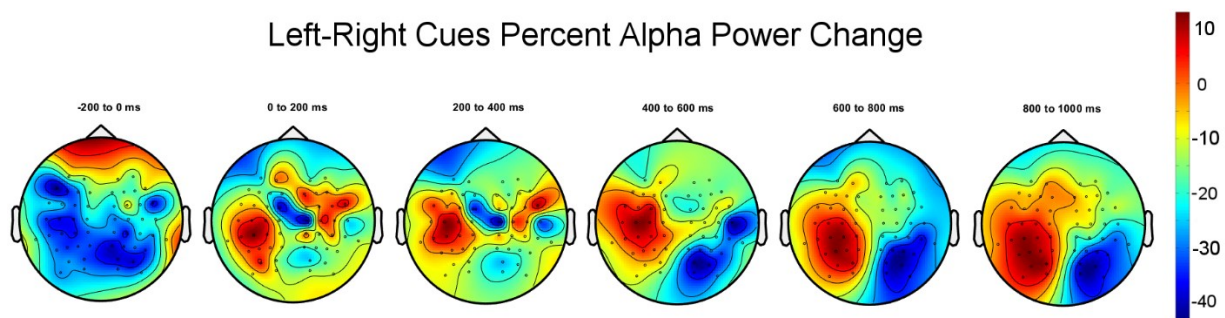


Figure 3.11. Scalp maps across time of the difference in alpha power percent change for left minus right cues in the 80/20 Experiment.

Experiment 2b - 50/50 Targets

ERPs to targets:

Plotted in Figure 3.12 and 3.13 are the grand mean ERPs contrasting the valid and invalid trials from -200 to 400 ms post target onset at 15 representative scalp sites for left and right visual field targets. As can be seen, all three early ERP components (C1, P1 and N1) are visible in both of these figures.

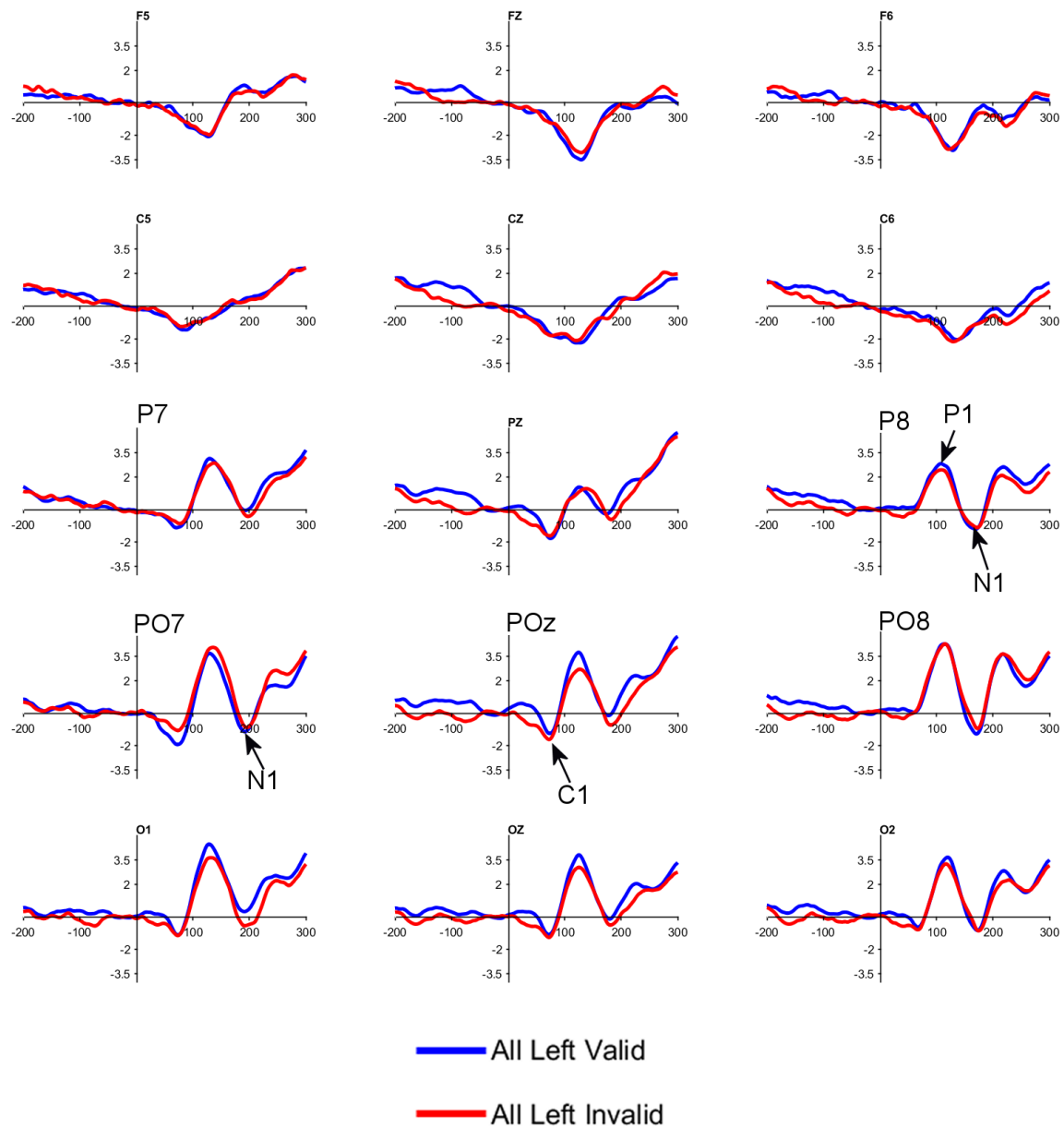


Figure 3.12. The grand mean Validity effect for left sided target trials across all 22 participants at 15 electrode sites. Positive plotted up in this and all subsequent ERP figures.

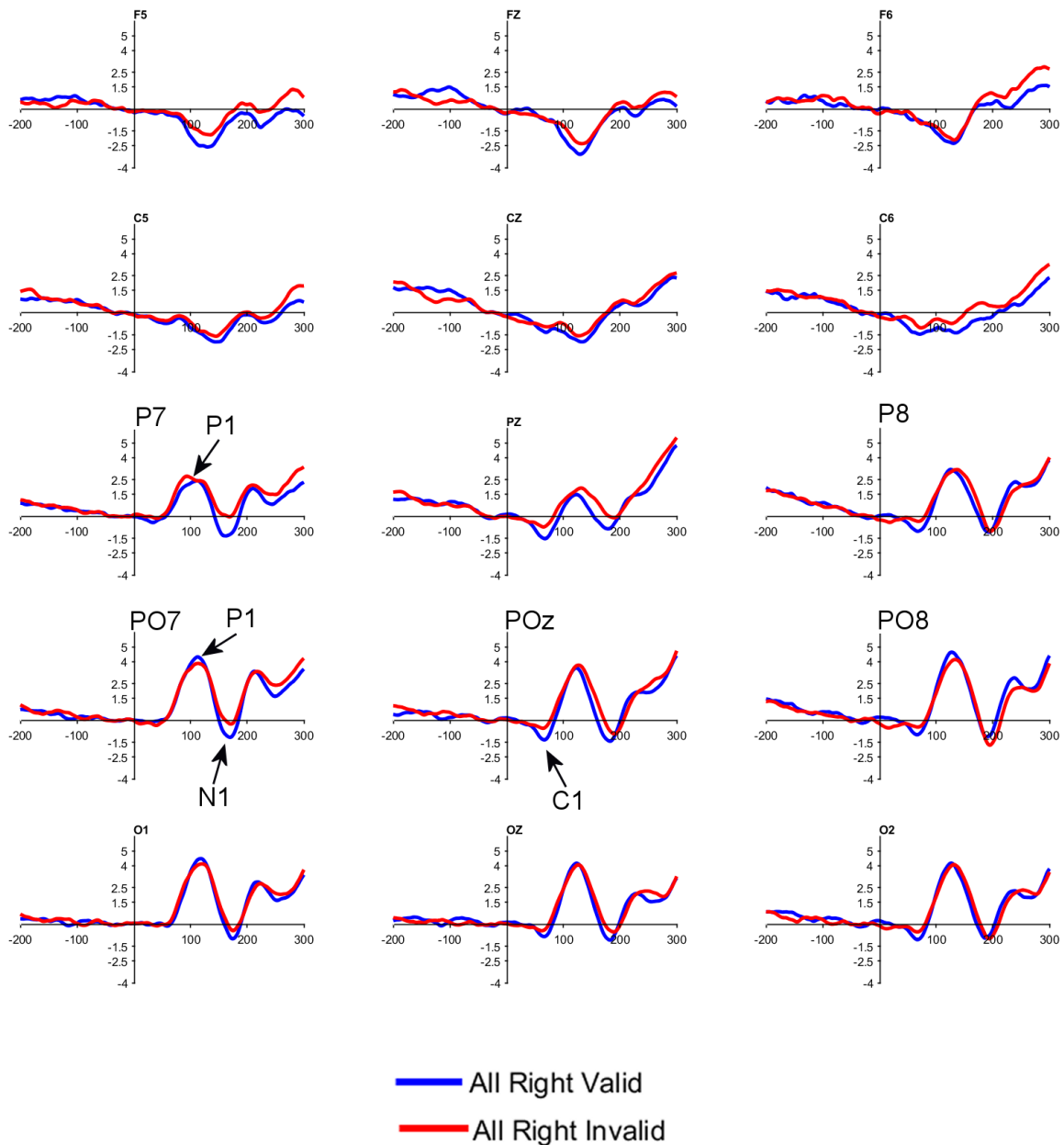


Figure 3.13. The grand mean Validity effect for right sided target trials across all 22 participants at 15 electrode sites.

C1 amplitude (40-80 ms)

In this epoch there were no significant main effects of Validity ($p > .42$) nor interactions of Validity and MSType ($p > .14$) in the omnibus ANOVA. However, in the planned follow-ups there was a significant Validity effect for the Congruent MSType ($F(1,21) = 10.15$, $p = .004$ –

see Figure 3.14) but not for either the Incongruent ($p > .59$) or No MSs ($p > .37$). As can be seen in Figure 3.14 Targets following valid cues produce a more negative C1 following congruent MSs with much smaller differences (albeit in the same direction) for the other two MStypes.

P1 amplitude (80-120 ms)

As can be seen in Figure 3.15 there was little evidence of a validity effect in this epoch at either the P7/8 or PO7/8 electrode sites. While the interaction between validity and MStype was not significant ($p = .4$), following the logic from Experiment 2a, we nevertheless did the planned comparisons of the validity effect for each of the MStypes separately. Statistical evaluation of the Validity effect did show a significant P1 effect for the Congruent MStype ($F(1,21) = 4.88$, $p = .04$) but not the other two MStypes (both $ps > .76$). The Congruent MStype Validity effect can be seen on the P1 in Figures 3.16 and 3.17 which plot the Validity effect separately for the three MStypes. The top panel in each figure shows that P1 amplitude does vary as a function of Validity but in most of the plots it was the **invalidly** cued targets that have the larger P1.

N1 amplitude (140-200 ms). In this epoch there was a clear N1 component and as can be seen in Figure 3.19, valid trials produced a significantly more negative N1 compared to invalid trials contralateral to the target, $F(1,21) = 5.41$, $p = 0.03$). Again, while the interaction between validity and MStype was not significant ($p = .32$), because our a priori predictions were primarily focused on the question of validity effects in the congruent (as opposed to incongruent) condition as outlined in the Methods and as done in Experiment 2a, we nevertheless did the planned comparisons of the validity effect for each of the MStypes. Likewise, there was a significant effect of Validity for targets preceded by congruent MSs ($F(1,21) = 9.4$, $p = 0.006$). As can be seen in Figures 3.16 and 3.17 this effect was due to the valid targets having a larger

N1 than invalid targets. There were no significant effects of Validity for the incongruent or no MS conditions ($p > .25$).

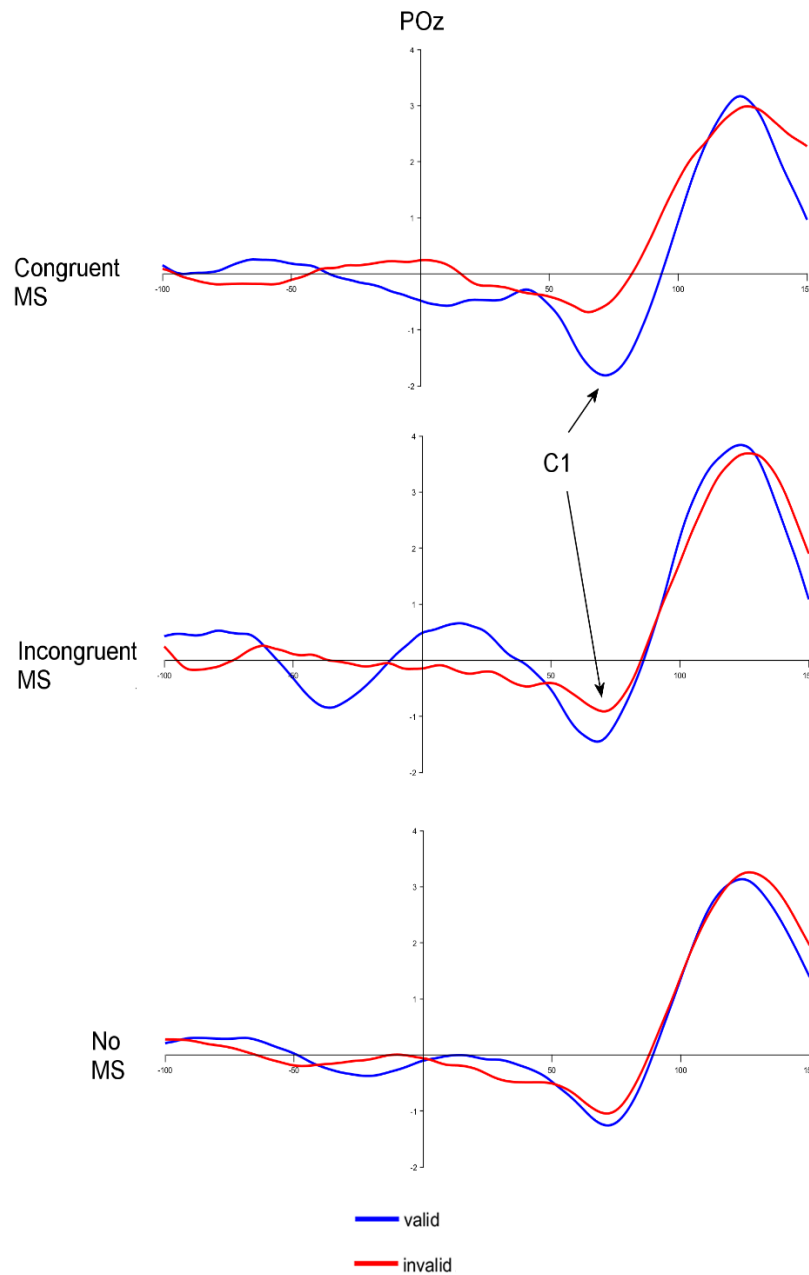


Figure 3.14. Main effect of Validity for the three MS types at POz. (right)

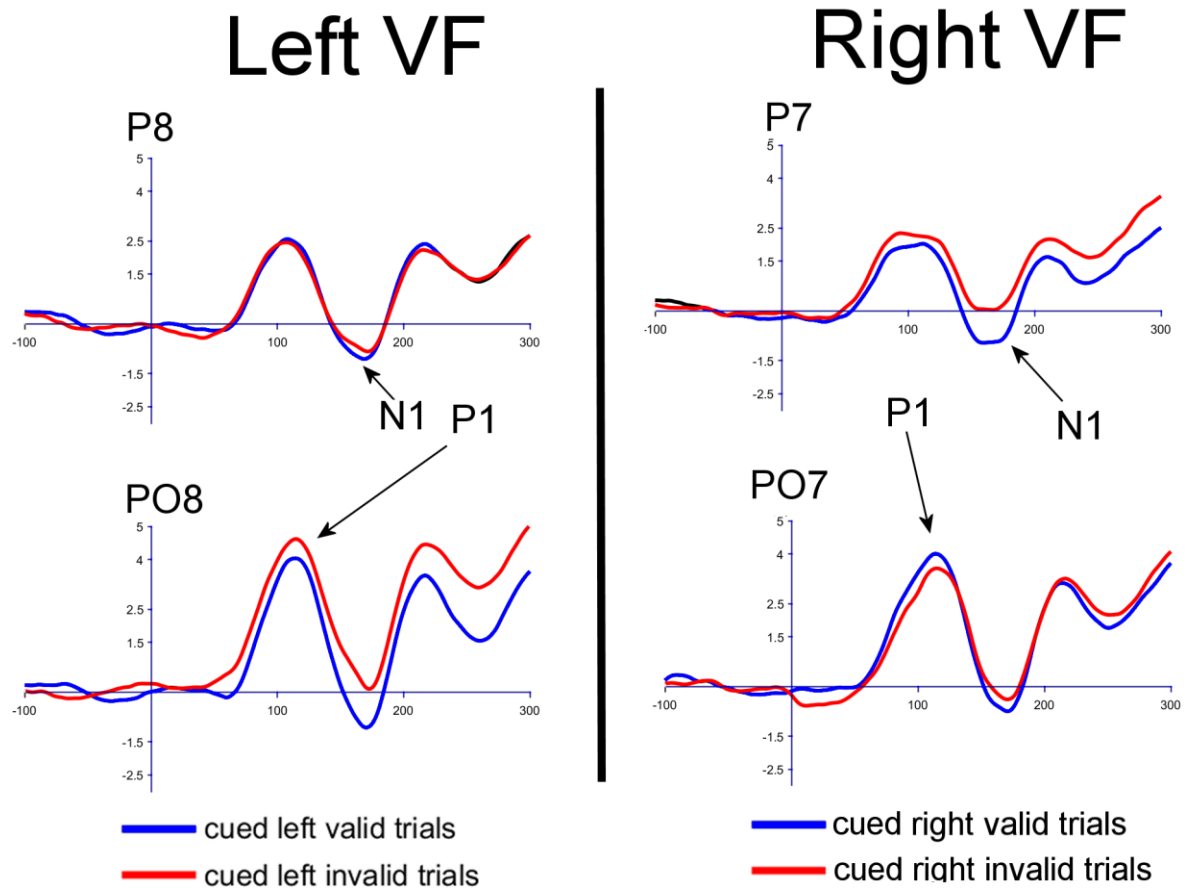


Figure 3.15. ERPs (-100 to 300 ms) for left and right VF targets contrasting the Valid and Invalid conditions at electrode sites contralateral to the side of target presentation.

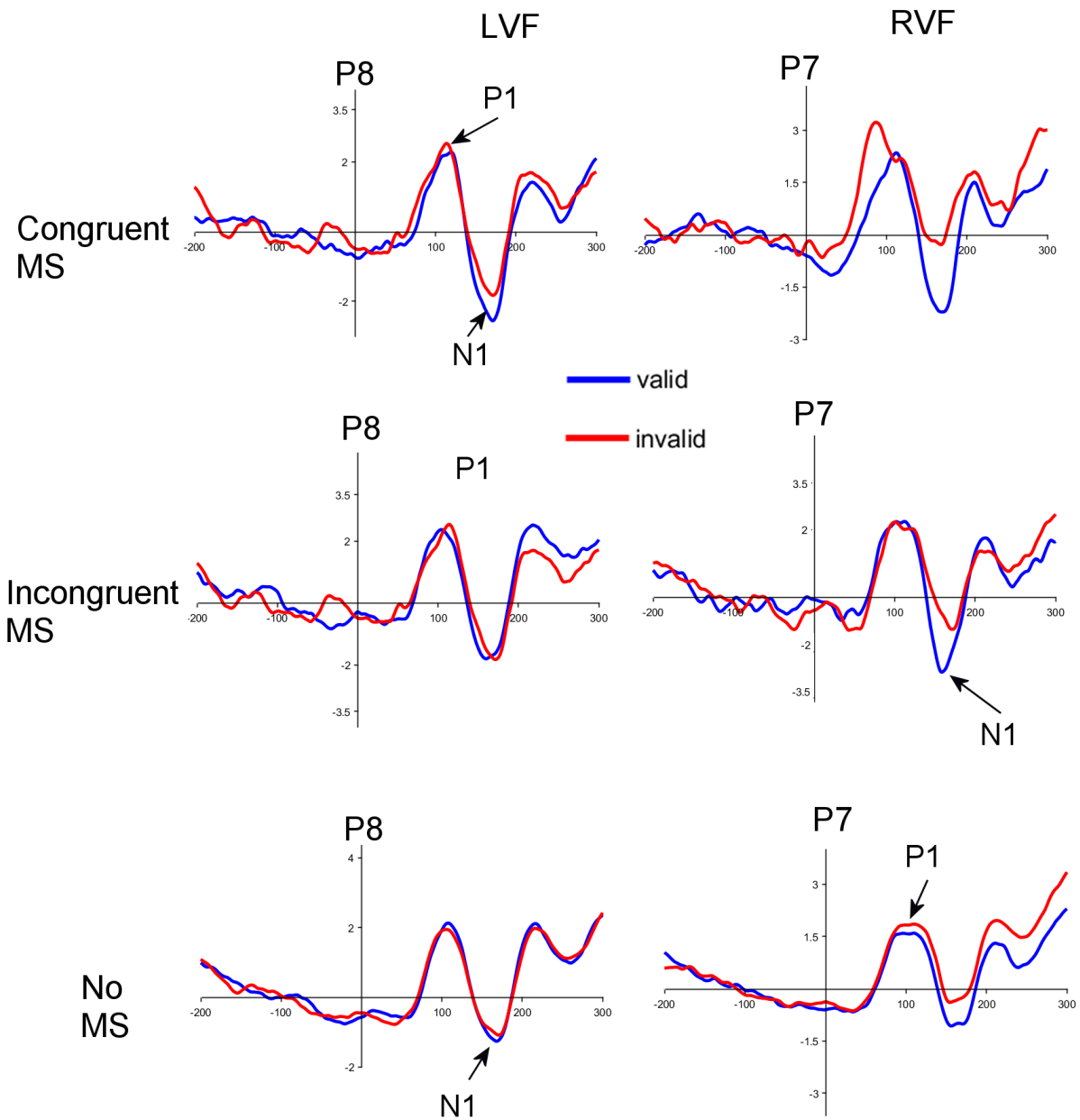


Figure 3.16. Contralateral ERP validity effects at the P7/8 sites as a function MSType.

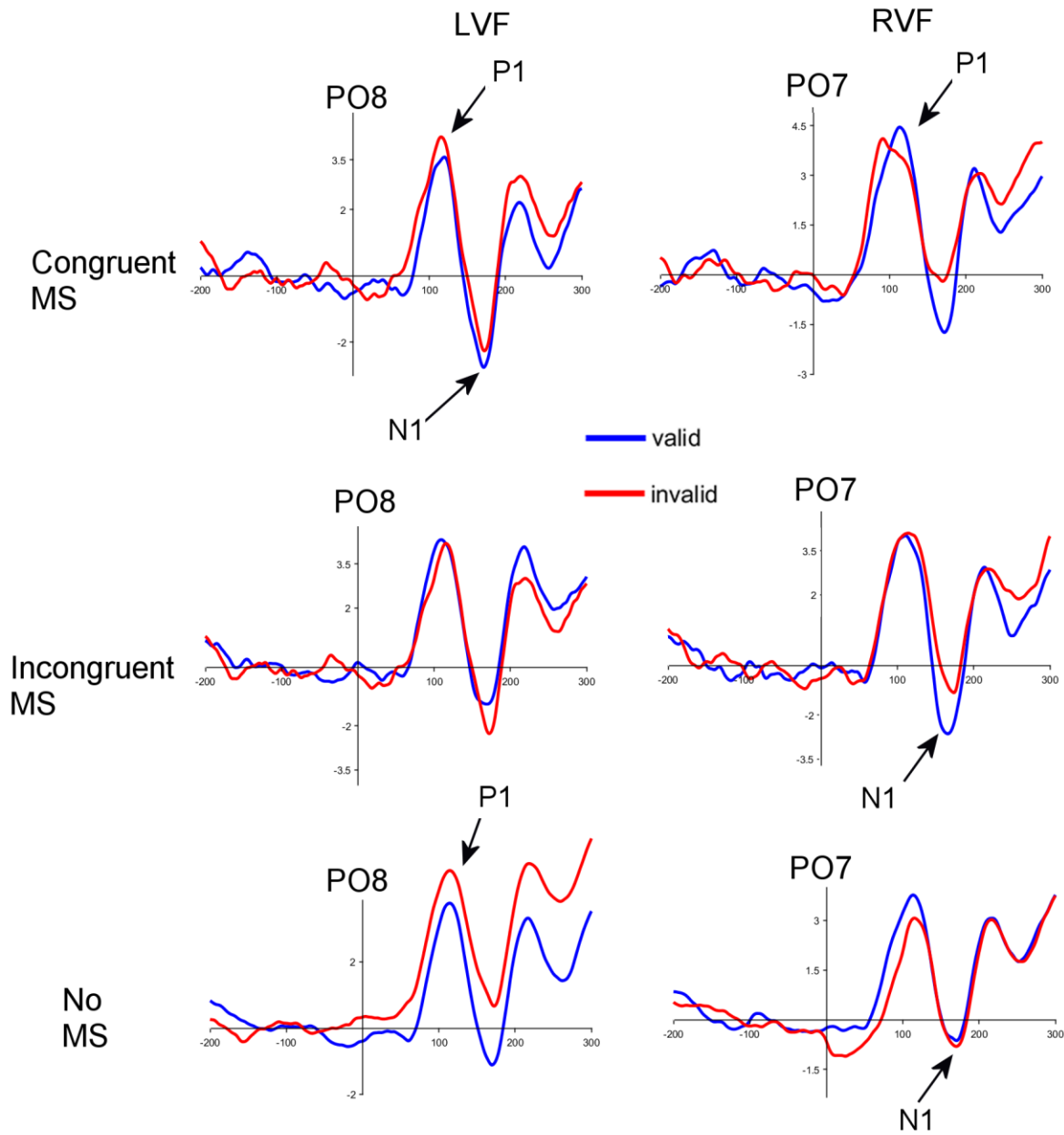


Figure 3.17. Same as Figure 3.20 but for the PO7/8 sites.

Target Alpha Power Percent Change:

While there was no significant Validity x MSType interaction ($p = .22$), planned comparisons were nonetheless investigated. Plotted in Figure 3.18 are the alpha power percent change graphs for the Validity effect for contralateral stimuli in the three MSType conditions.

The only significant effect for the contralateral target-locked alpha power was for the no MS condition where there was more alpha power decrease (i.e., more alpha desynchronization) for invalidly than validly cued trials ($F(1,21) = 6.77, p = 0.017$). There were no significant effects for the incongruent contralateral validity effect ($ps > .76$), but there was a marginal Validity effect for the congruent MS condition ($F(1,21) = 3.97, p = 0.06$). However, this latter effect was like the no MS condition in the opposite direction with invalid trials producing greater alpha desynchronization than valid trials (-20% vs. -6%).

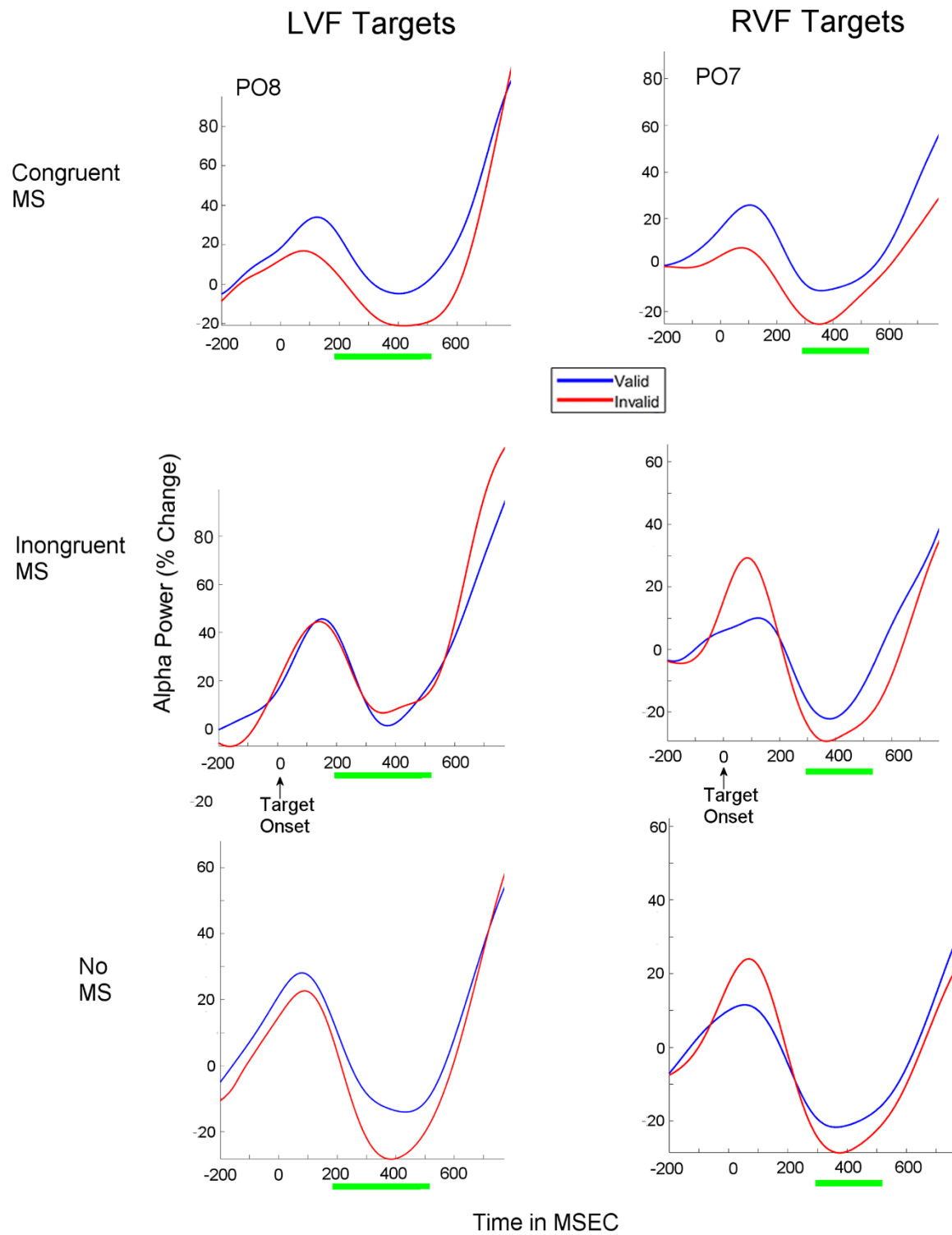


Figure 3.18. Contralateral target alpha power Validity effect in Experiment 2b for the three MSTypes.

Cue-locked Alpha Power Percent Change:

Plotted in Figure 3.19 are the time course functions of alpha power percent change for left (blue) compared to right (red) cues at 4 electrode sites. Plotted in Figure 3.20 across several time epochs are the alpha power change scalp maps computed from the difference between the left and right cues. The analysis of these data showed a Cue side by Electrode laterality effect in the 600-800 ms epoch ($F(1,21) = 9.13$, $p = 0.007$ - see Figure 3.19).

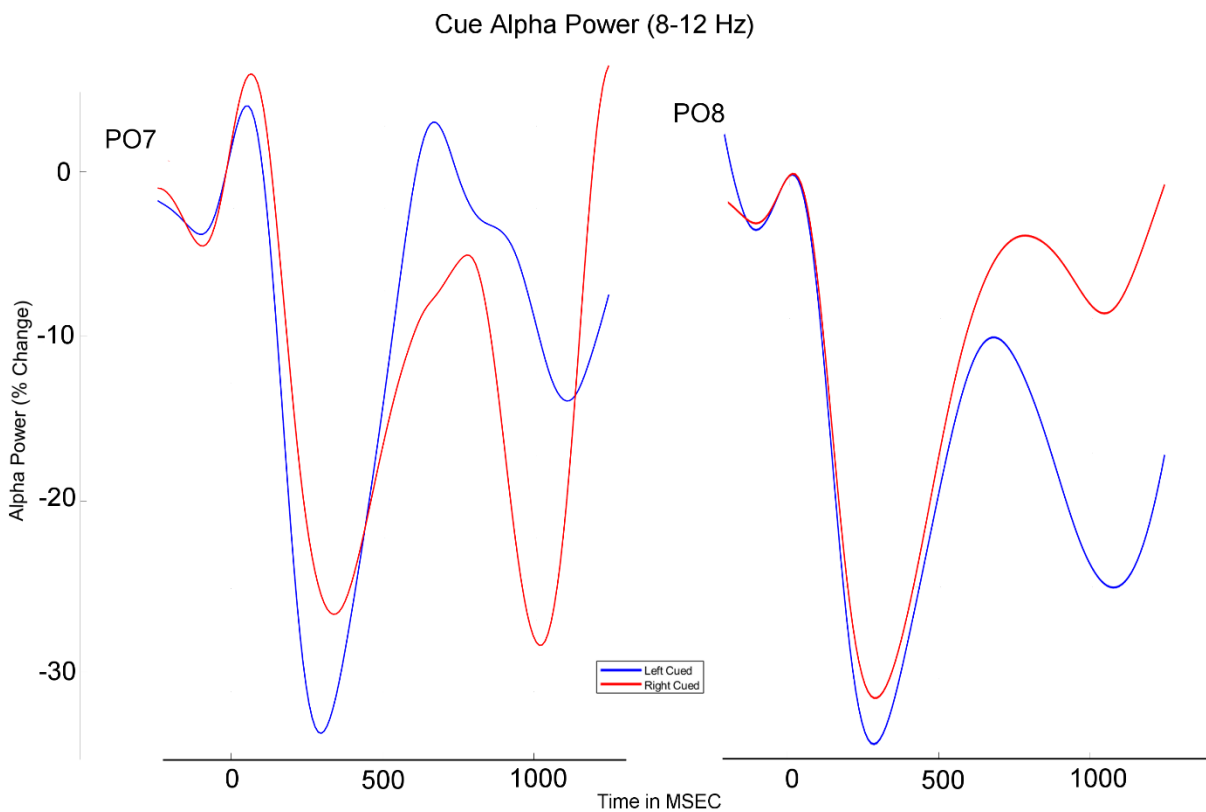


Figure 3.19. Time course of alpha power percent change to left and right cues at PO7 and PO8.

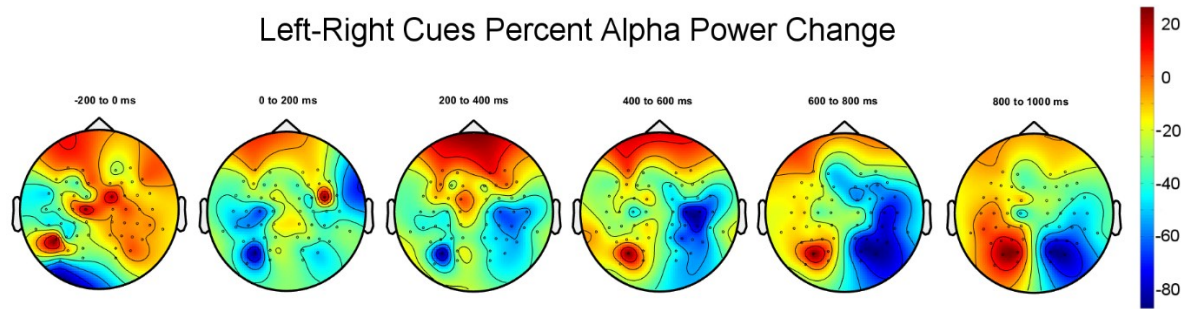


Figure 3.20. Scalp maps across time of the difference in alpha power percent change for left minus right cues in the 50/50 Experiment.

Experiment 2a vs. 2b Comparisons

In the analyses in section the Validity effect from differences waves (valid – invalid) in each of the three component epochs of interest were compared between the two Experiments (2a vs. 2b).

C1 Validity Effects

There was a main effect of Experiment ($F(1,38) = 5.94$, $p = 0.02$) with a larger C1 attention effect (i.e., more negative for valid than invalid) for the 50/50 Experiment (see Figure 3.21).

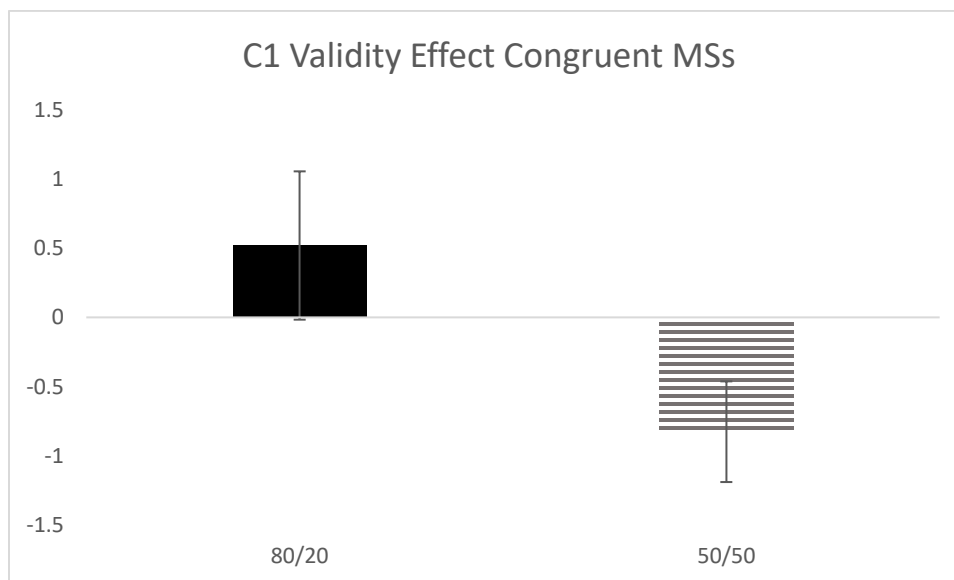


Figure 3.21. C1 attention effect for the two experiments.

P1 Validity Effects

There was also a significant Experiment ($F(1,38) = 11.84, p = 0.001$) Validity effect for congruent MSs but there were no comparable effects for the incongruent and No MS conditions ($ps > .38$). As can be seen in the Figure 3.22, the P1 congruent MS validity effect was larger in the 80/20 experiment.

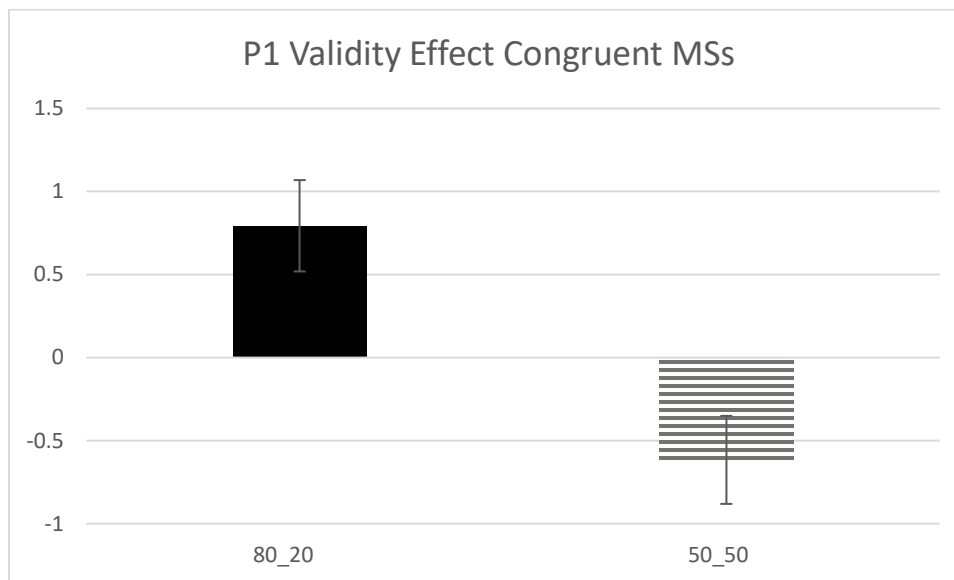


Figure 3.22. The P1 Validity effect contrasted for the two experiments.

N1 Validity Effects

There were no N1 validity effect differences as a function of Experiment (all $ps > .06$).

Discussion

This analysis investigated the relationship between microsaccades and attention across two experiments that differed in the predictability of the spatial cue. While there was no evidence of the predicted C1 attention effect in Experiment 2a, the classic covert spatial attention contralateral effects on early visual ERPs (P1/N1) were observed, as expected. Crucially, the C1

component did not differ as a function of attention depending on MStype, contradicting the original (minority view) hypotheses. Puzzlingly, there was a C1 attention effect following congruent microsaccades; this effect was not significant for the incongruent or no MS conditions.

While the omnibus tests in both experiments indicated no significant interactions between validity and MStype factors, we nevertheless went ahead with the planned comparisons given the importance of these contrasts to the hypothesized impact of MStype on attention.

Interestingly, when parsed by MStype, a P1 contralateral attention effect was observed for congruent MSs. This same contrast was not significant for the incongruent or no MS conditions.

A similar pattern was observed in the target-locked alpha power analyses. Congruent microsaccades were associated with less target-locked alpha power contralateral to the target side, but did not differ for the other two microsaccade conditions. Further confirming that the participants used the cue information to predict subsequent target side, cue-locked alpha power decreased contralateral to the cued-side.

For Experiment 2b, where cues were non-predictive (although participants were told the cues would help their performance), the C1 component was significantly enhanced on valid compared to invalid trials. Furthermore, upon examining the effects of MStype, when congruent MSs were made, the C1 response was greater in amplitude, while no effect was observed for incongruent or no MS trials. As expected, there were no validity effects on the P1 component. However, there was a validity effect for the N1 component epoch, where valid trials produced a larger negative-going N1 contralateral to the target side compared to invalid trials. Similar to Experiment 2a, in planned follow-up analyses the N1 contralateral attention effect was observed for congruent MSs but not for incongruent or no MS conditions. Finally, cue-locked alpha power

indicated participants were indeed attending towards the cued-side, as less alpha power (i.e. more desync) was observed on the contralateral electrodes.

Overall, these findings show effects of cue validity on EEG and ERPs time-locked to targets, as well as some evidence that predictive cues are associated with enhanced P1 and N1 ERPs when congruent microsaccades precede the target. On the other hand, because there were no significant MStype by Validity interactions for any of the dependent measures, we cannot conclude that there are meaningful differences in attention as a function of MStype. While not conclusive, this pattern does suggest a possible link between attention and microsaccades.

Chapter 4: Study 3

Introduction

The investigation of individual differences in visual working memory (VWM) capacity is predicated on the theoretical framework that defines VWM not merely as a passive storage buffer, but as a core executive function essential for the top-down control of selective attention (Gazzaley & Nobre, 2012; Kane et al., 2001). A hypothesized isomorphism has been proposed between VWM capacity and the mechanism of input selection, which involves the prioritization of task-relevant information for further cortical processing while simultaneously filtering out irrelevant distractors (Luck & Gold, 2008). This relationship is theoretically grounded in the observation that both systems utilize shared neural architecture within the DAN (particularly FEF and IPS) to maintain a stable focus of attention (Awh & Jonides, 2001; Corbetta & Shulman, 2002; Kastner et al., 1999). Crucially, filtering paradigms have revealed that individuals with high VWM capacity exhibit a superior ability to selectively exclude irrelevant information from this memory store (McNab & Klingberg, 2008; Vogel et al., 2005; Zanto &

Gazzaley, 2009). Empirical evidence from behavioral studies has substantiated the link between individual differences in VWM capacity and the precision of attentional biasing (Bleckley, Durso, Crutchfield, Engle, and Khanna, 2003; Kane, Bleckley, Conway, & Engle, 2001). High-capacity individuals demonstrate greater stability in their attentional set and are significantly more effective at resisting attentional capture by salient but irrelevant peripheral events (Gaspar, Christie, Prime, Jolicœur, & McDonald, 2016; Fukuda & Vogel, 2009).

The exertion of top-down control over the oculomotor system is manifested in the systematic inhibition of microsaccades during periods of high attentional demand or anticipatory task preparation (Denison et al., 2019; Pastukhov & Braun, 2010). In this context high-VWM individuals are better able to deploy these top-down signals to maintain fixation stability (Kane et al., 2001; Unsworth et al., 2004), using a process mediated by descending projections from the FEF that bias neural competition in the SC and visual cortex (Merrikhi et al., 2017; Pouget et al., 2009). As a result, when individuals are tasked with maintaining a stable attentional set, microsaccade rates typically decrease, with the remaining eye movements becoming significantly more informative about the location of the internal focus of attention (Denison et al., 2019; Pastukhov & Braun, 2010). In this way high-VWM individuals are hypothesized to possess a superior ability to suppress task-irrelevant or random oculomotor noise, reflecting a more robust internal selection template that prevents the "leakage" of attentional shifts into peripheral motor outputs (Gaspar et al., 2016; Kane et al., 2001; Unsworth et al., 2004). Similarly, individual differences in WM capacity have been shown to predict lower-level sensorimotor abilities, specifically saccade control, suggesting that the executive resources required for memory maintenance are the same resources used to regulate the oculomotor system (Kane et al., 2001; Unsworth et al., 2004).

The core research question in this chapter was whether individual differences in VWM capacity—defined as a core executive function for top-down control— would predict systematic variations in the neural signatures of covert spatial attention (Gaspar et al., 2016). More specifically, the experiments reported here sought to determine if high-capacity individuals, who are hypothesized to possess more efficient neural filtering, would because of more temporally precise and sustained congruent microsaccadic biasing, show greater spatial attention effects thereby establishing VWM capacity as an important driver of the variability in the neural and oculomotor signatures of attention (Gaspar et al., 2016; Gazzaley & Nobre, 2012; Kane et al., 2001; Vogel et al., 2005).

The current experiments were primarily focused on whether the potentiation of early cortical gain, specifically measured via the C1 ERP, is contingent upon the subject's executive control (Kelly et al., 2008; Rauss et al., 2009; Zanto & Gazzaley, 2009). Although there were no observed C1 effects in Experiment 2a (Chapter 3) the analysis in this chapter sought to determine if that failure to find the earliest of attention effects on the C1 was due to VWM capacity (see Guiliano, Karns, Neville, & Hillyard, 2014). Specifically, it was hypothesized if C1 spatial attention effects are real (the minority view), then High-VWM participants would be the most likely to show this kind of effect and furthermore that it might have been the low-VWM participants in Experiment 2a that resulted in null C1 attention effects. Likewise, it was hypothesized that High- compared to Low-VWM individuals would show a behavioral (RT and perhaps accuracy) attention difference. Given the significant P1 spatial attention effects in Experiment 2a and the similar effects on the N1 in both Experiments 2a and 2b, it was also predicted that VWM would modulate the size of these attention effects as well. Following from the predictions on the C1, here it is hypothesized that the high-VWM group in Experiment 3a

(80/20 validity manipulation) would show larger P1 and N1 attention effects than the low-VWM participants. Likewise, in Experiment 3b (50/50 validity manipulation) it was hypothesized that the high-VWM participants would generate a larger N1 attention effect than the low-VWM participants.

In the two experiments in this chapter data from participants in Chapter 3 were reanalyzed by dividing participants into two groups (High- and Low-VWM) based on their scores on a challenging subtest of VWM (the CDT 8 item subtest). In both experiments (3a 80/20 and 3b 50/50) participants were divided at the median CDT8 score and the resulting, behavioral (RT and accuracy) eye-tracking and EEG/ERP data were reanalyzed.

Methods

Participants

All but one participant used in the previous chapter (Chapter 3) were used here due to missing data (*Experiment 3b*).

Experiment 3a: Twenty healthy right-handed human volunteers participated in this study (19.5 ± 1.76 years of age, 14 females, three corrected-to-normal vision with contact lenses). Three volunteers were not included in the final data set either because they only completed one of the required two recording sessions, four failed to achieve the criterion accuracy in the spatial attention task. Another four volunteers were not included in the final dataset due to their inability to follow task instructions adequately (i.e. holding their eyes on the central fixation dot).

Experiment 3b: Twenty-one healthy right-handed human volunteers participated in this study (19.86 ± 2.2 years of age, 18 females, five corrected-to-normal vision with contact lenses). Three volunteers were not included in the final data set either because they only completed one of the

required two recording sessions, two failed to achieve the criterion accuracy in the spatial attention task, and four had significant trials rejected due to excessive EEG artifact or data errors. Another three volunteers were not included in the final dataset due to their inability to follow task instructions adequately (i.e. holding their eyes on the central fixation dot).

Stimuli and Experimental Paradigm

Change detection task: Participants performed a color change detection task (see Figure 4.1). A memory array of colored squares ($1^\circ \times 1^\circ$ of visual angle, from a viewing distance of 90 cm) appeared for 100 ms around a black fixation dot (4 arcminutes) at the center of a grey (RGB values: 0, 0, 0) screen. Items were randomly selected without replacement from a set of nine discriminable colors: red, magenta, blue, cyan, green, yellow, orange, brown, and black.

Participants were instructed to memorize the squares' colors. The squares disappeared for a 300-700 ms (mean 500 ms) retention interval (leaving only the fixation dot), and then another array with the same number of colored squares, each appearing in the same spatial locations as the memory array, appeared. On 50% of the trials one of the colored squares changed colors, while 50% of the time the retention array was identical to the memory array. Participants were instructed to respond with either the left or right arrow key (counter-balanced across participants) if the color changed, while the other key if no colors changed. Participants completed a total of 240 trials, divided evenly among three set-size conditions (80 trials each for arrays of 2, 4, or 8 simultaneously presented squares). The squares could appear anywhere within a region subtending $\pm 7.0^\circ$ of visual angle from central fixation. Stimulus positions were randomized on each trial, with the constraint that items were separated by a minimum center-to-center distance of 2.0° of visual angle on at least one axis to prevent overlapping.

Attention task: See Chapter 2 methods.

Eye-Tracking Methods

See Chapter 2 methods.

EEG Methods

See Chapter 3 methods.

Working Memory Analysis: Data from participants in Chapter 3 were reanalyzed by dividing participants into two groups based on their scores on the most challenging subtest of VWM capacity, where eight items were simultaneously presented (the CDT 8 item subtest; see Figure 4.1). In both experiments (3a 80/20 and 3b 50/50) participants were divided at the median CDT8 score and the resulting behavioral (RT and accuracy), eye-tracking and EEG/ERP data were analyzed. Separate GLM mixed-design ANOVAs were performed using Group (High- or Low-VWM scores) as the between-subjects factor and the same repeated-measures factors as described in Chapters 2 (MSType) and 3 (EEG/ERP). Because of the importance of validity effects for the different MSTypes and now VWM group, as in Chapter 3, omnibus ANOVAs were followed up with specific planned comparisons for each MSType and VWM group.

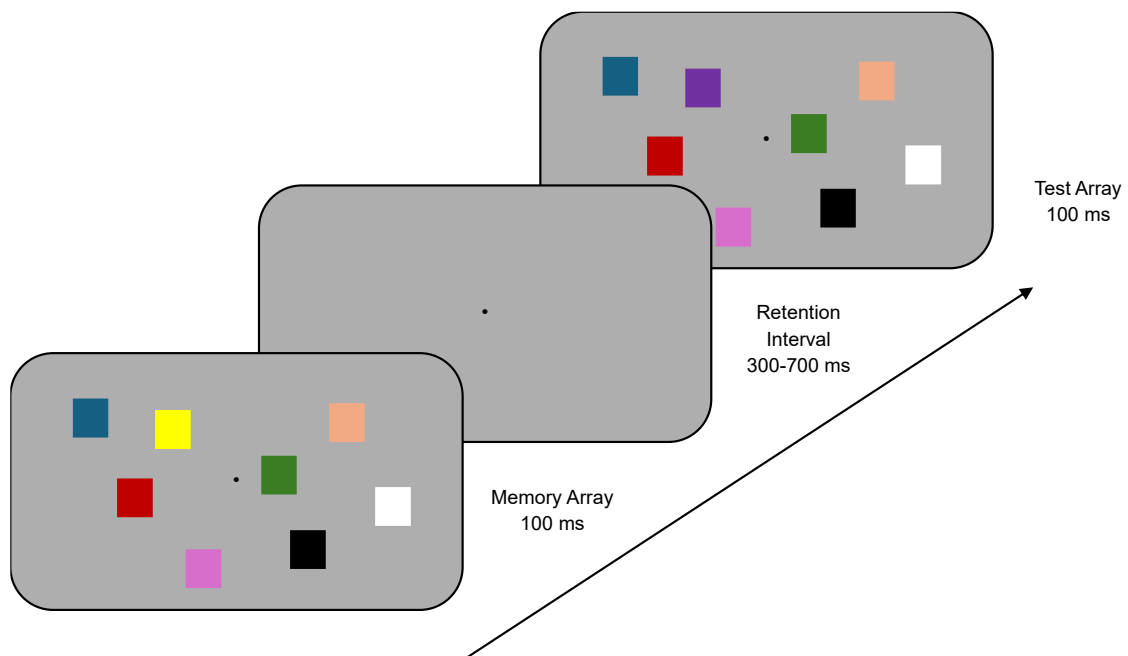


Figure 4.1. Change detection task visual working memory task. Participants were instructed to remember the colors of the colored squares (2, 4, or 8 presented simultaneously), and after they disappeared for a brief period, participants would press one arrow key if any of the squares changed color (50% of trials) and another if they did not.

Participant	TwoItemRT	TwoItemACC	FourItemRT	FourItemACC	EightItemRT	EightItemACC
1	1.157870284	0.771084337	1.245216815	0.746987952	1.219854464	0.488095238
2	1.35213121	0.541176471	1.377008865	0.614457831	1.356437961	0.5
3	1.207478711	0.821428571	1.291553728	0.707317073	1.269058107	0.630952381
4	1.368496232	0.564705882	1.353656688	0.43902439	1.36114764	0.542168675
5	1.329911195	0.619047619	1.37081574	0.554216867	1.292457634	0.578313253
6	1.320987338	0.488095238	1.352860357	0.580246914	1.315746318	0.458823529
7	1.296506881	0.882352941	1.354936938	0.777777778	1.390800566	0.523809524
8	1.244635494	0.705882353	1.316948831	0.670731707	1.370771	0.542168675
9	1.247895735	0.5	1.25432143	0.578313253	1.206302235	0.590361446
10	1.195466333	0.929411765	1.234942	0.790123457	1.323741265	0.726190476
11	1.267761531	0.654761905	1.315445383	0.638554217	1.388627357	0.602409639
12	1.263642877	0.666666667	1.336283895	0.542168675	1.26050791	0.554216867
13	1.306717494	0.611764706	1.317429449	0.691358025	1.377965543	0.44047619
14	1.115314104	0.56626506	1.041725342	0.493975904	0.988157091	0.535714286
15	1.161087651	0.928571429	1.225897317	0.719512195	1.227054542	0.5
16	1.285870214	0.8	1.290787642	0.792682927	1.328581193	0.65060241
17	1.221054329	0.843373494	1.261171214	0.678571429	1.216929878	0.518072289
18	1.284003524	0.714285714	1.307113545	0.695121951	1.330470093	0.55952381
19	1.243830482	0.752941176	1.316963987	0.695121951	1.314242163	0.602409639
20	1.299667145	0.752941176	1.321448052	0.578313253	1.347901778	0.597560976

Table 4.1. Accuracy and RTs for Two, Four, or Eight items for change detection task per participant for *Experiment 3a*.

Results

Experiment 3a 80/20

Table 4.1 reports accuracy and RTs for the Two, Four, or Eight items for change in the VWM change detection task for Experiments 3a.

Behavioral Results:

Analysis of the RT data revealed a main effect of Validity as reported in Chapter 3. And while there was not a significant interaction between Validity and WM group in the omnibus analyses, follow-ups as a function of VWM subgroup revealed a significant main effect of validity in the high but not the low VWM subgroup (main effect of validity high: $F(1,19) = 17.33$, $p = 0.002$; low: $p > .16$). Further follow-up analyses demonstrated that the bulk of the

Validity effect in the high VWM group was carried by the congruent MS condition as shown by the significant Validity effect in this sub-analysis (congruent MS main effect of Validity: $F(1,18) = 10.45, p = 0.005$). There were no differences in RTs as a function of VWM group and Validity for the incongruent or no MS conditions ($ps > .34$). These differences can be seen in Figure 4.2 (left) the high VWM group produced a larger Validity RT effect following congruent MSs than the low (4.2 right) VWM group. There were also no differences in accuracy as a function of VWM capacity ($ps > .5$ see Figure 4.3).

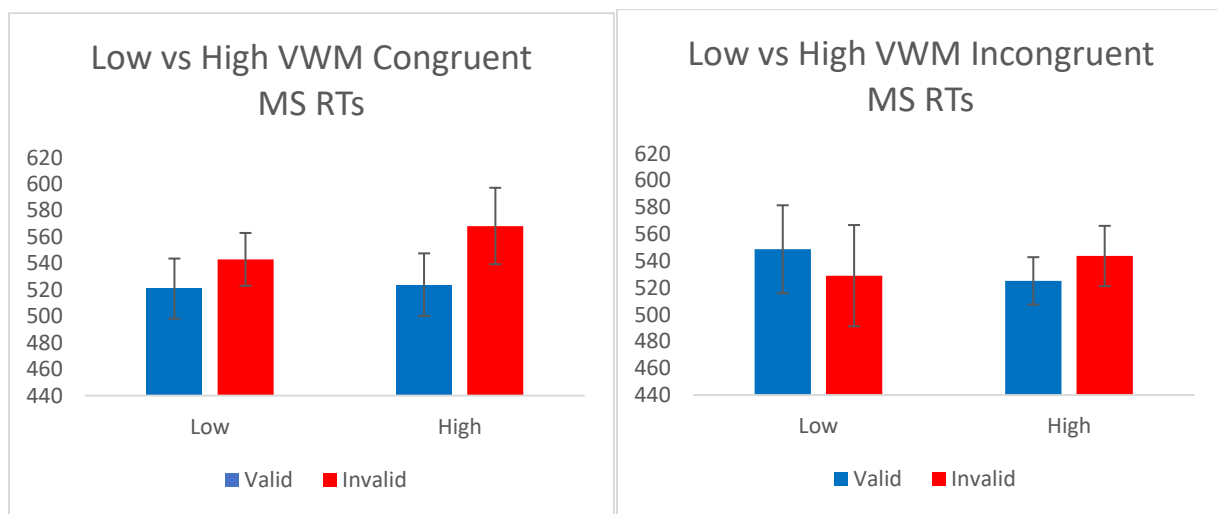


Figure 4.2 RTs for the congruent MS (left) and incongruent MS (right) conditions for the two VWM subgroups in Experiment 3a.

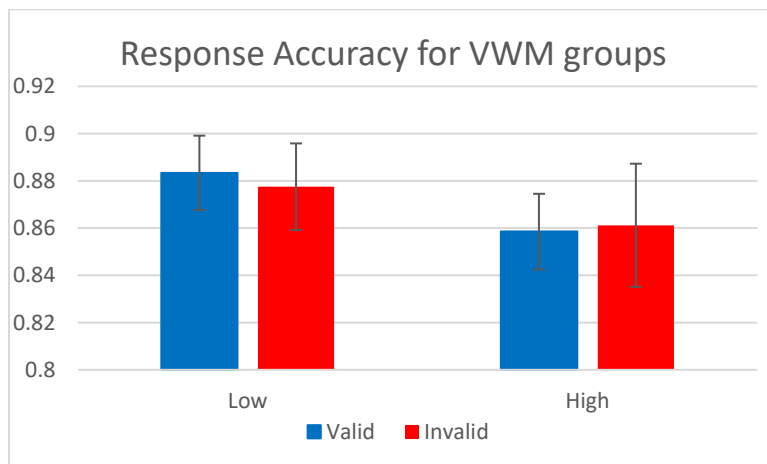


Figure 4.3 Accuracy as a function of VWM group in Experiment 3a.

Eye-Tracking

Rate, amplitude and direction

For MS rate comparing the two VWM groups in the 80/20 experiment only the MS data from the third measurement window (350-500 ms) was analyzed. For MS rate there was not a main effect of VWM group or VWM group x MStype interaction (p 's > .24), however, planned follow-up analyses looking at MS rate separately for each VWM group produced a significant congruency effect in the high ($F(1,9) = 7.32$, $p = .03$) but not the low VWM group ($p > .38$). As can be seen in Figure 4.4 Left, the congruency effect in the high group was due to a greater MS rate for congruent than incongruent MS. As was the case for MS rate, MS amplitude did not differ between the two VWM groups either as a main effect or interaction with Congruency. However, here there was also an absence of a significant MStype effects for either VWM group when analyzed separately (see Figure 4.5). Finally for differences in the direction of MSs (towards or away from the cue) only the high-VWM group showed significantly more MSs in the direction of the cue (mean = 74 vs. 64; $\chi^2 = 18.1$ (9), $p = .034$). The low-VWM group did not produce a significant difference ($p > .18$).

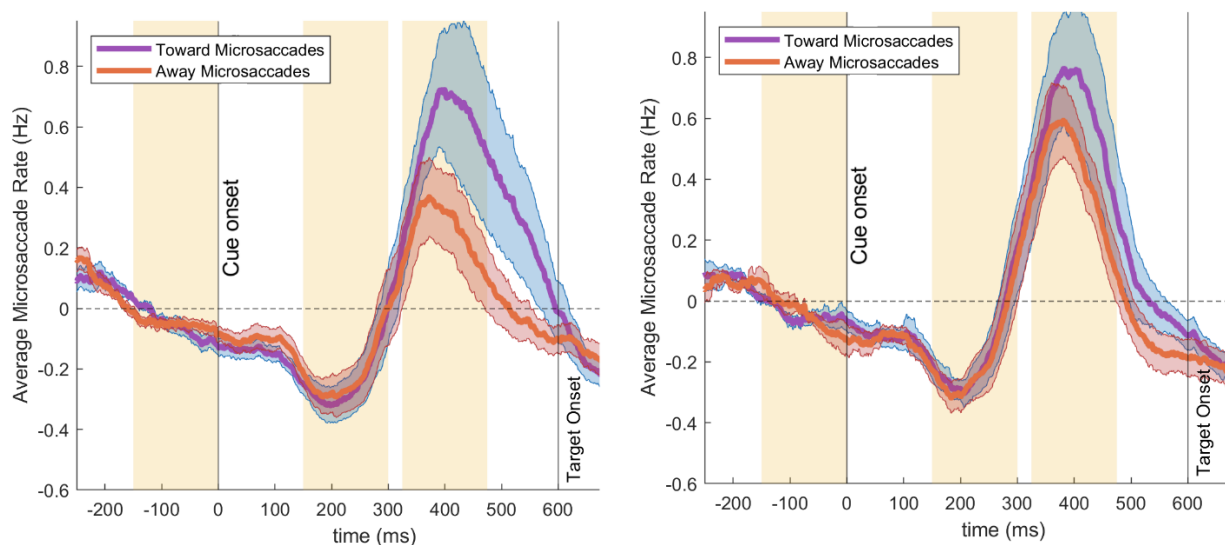


Figure 4.4 (left) cue MS rate for the High-VWM group (right) low-VWM group in Experiment 3a.

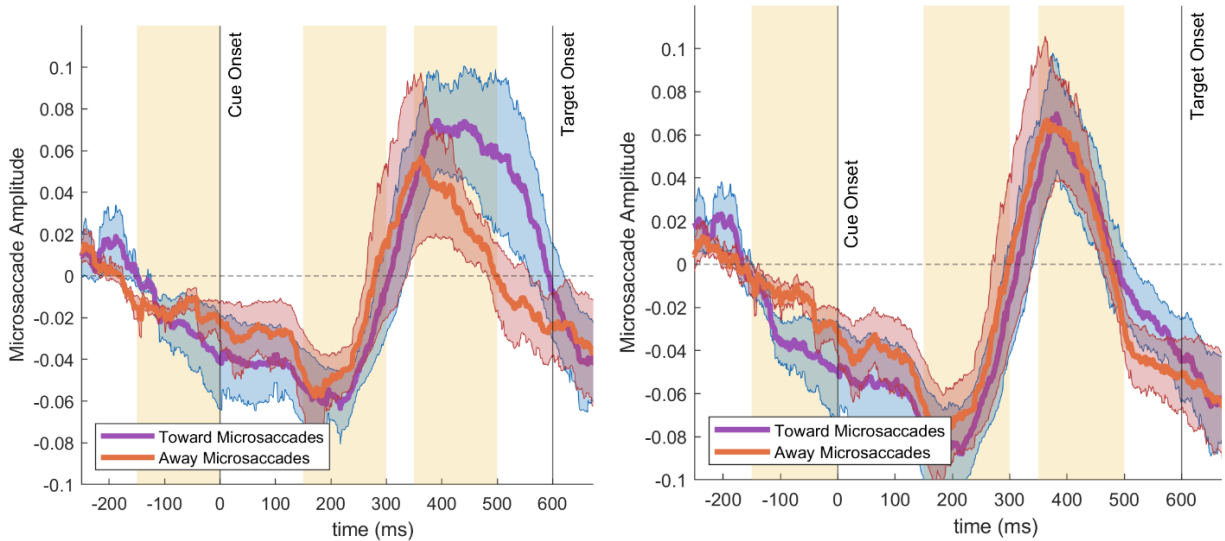


Figure 4.5 (left) cue MS amplitude for the High-VWM group (right) low-VWM group in Experiment 3a.

ERPs to targets:

Plotted in Figure 4.6 are the difference wave ERPs contrasting the Validity effect for the three MSTypes. The top panel is for the High-VWM group, and the bottom panel is for the Low-VWM group. Analyses of these data did not show any VWM effects impacting the C1 Validity effect (all p s > .3).

Analysis of the P1 epoch revealed a marginal main effect of validity ($F(1, 18) = 4.1$, $p = 0.056$), but there were no significant interactions involving the validity factor and the MStype and/or VWM group factors (all p 's > .12). However, in the planned follow-up analyses there was a Validity effect in the P1 epoch for the high-VWM group in the congruent MS condition ($F(1,19) = 18.06$, $p = 0.002$) with valid trials producing larger contralateral P1s than invalid trials. There was not a comparable effect in the low-VWM group ($p > .67$) as can be seen in

Figure 4.6 (bottom). The Validity effect was not significant in either group for the incongruent and no MS conditions (p s > .28).

For the N1 there was a main effect of validity ($F(1, 18) = 9.42, p = 0.007$) as reported in Chapter 3, and as was the case for the P1, there were no significant interactions involving the validity factor and the MStype and/or VWM group factors (all p 's > .11). In the planned follow-up analyses there were significant contralateral Validity effects for the High-VWM group for congruent MSs ($F(1,19) = 7.66, p = 0.0228$) with more negative N1s for valid than invalid trials (see top panel of Figure 4.6) but the Validity effect was only marginally significant for the incongruent ($p = .1$) and no MS ($p = .06$) conditions. In the case of the low VWM group there were only marginal contralateral validity effects in the congruent ($p = .053$) and no MS ($p = .06$) conditions and no significant effect for the incongruent MS condition ($p > .85$).

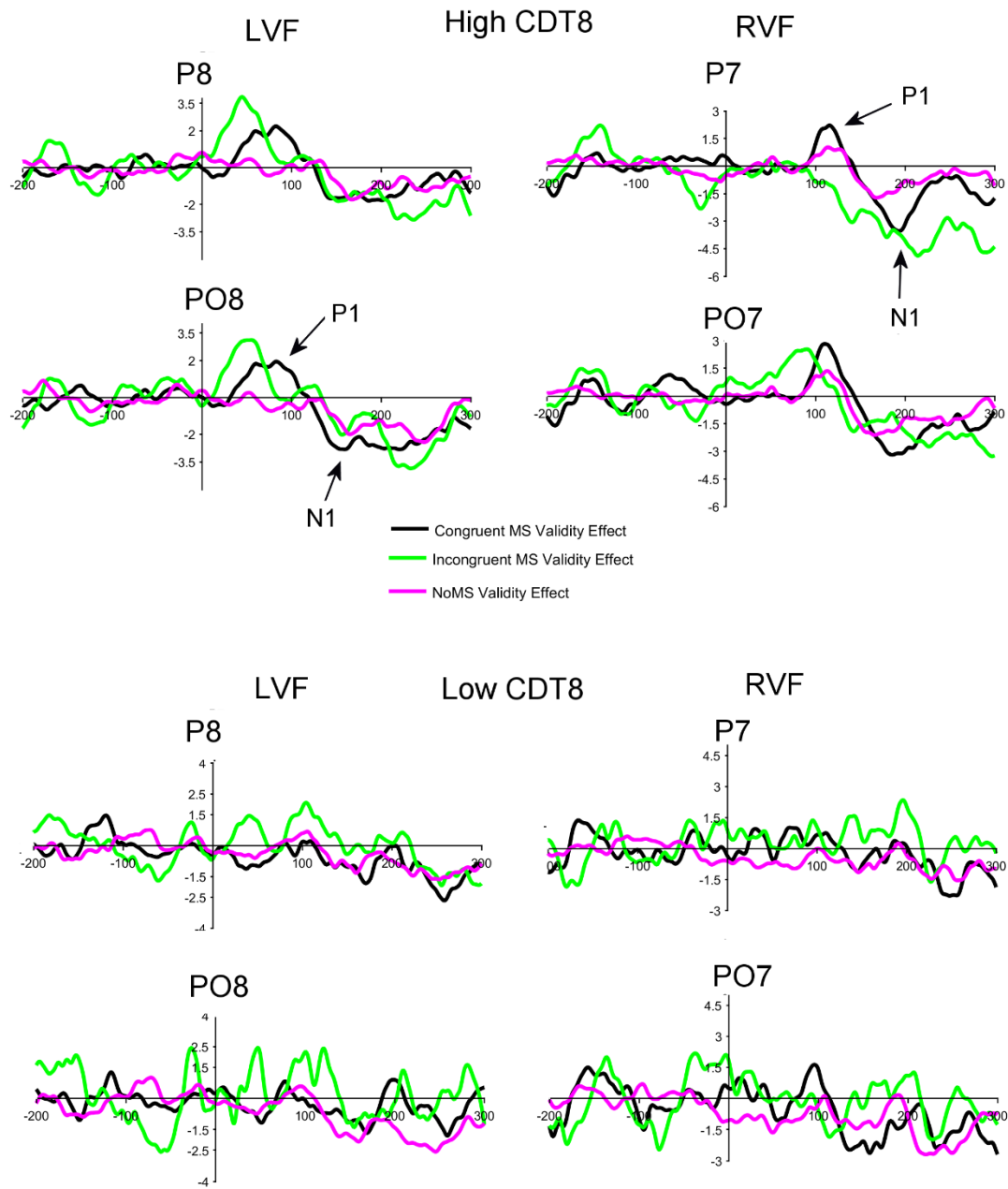


Figure 4.6 Validity effect difference waves for each MSType for the High (top) vs. Low (bottom) VWM groups in Experiment 3a.

Experiment 3b. Working Memory Target ERP Analysis 50/50

Table 4.2 reports accuracy and RTs for the Two, Four, or Eight items for change in the VWM change detection task for Experiments 3b.

Participant	TwoItemRT	TwoItemACC	FourItemRT	FourItemACC	EightItemRT	EightItemACC
1	1.244088	0.6	1.258963	0.542169	1.323857	0.487805
2	1.288424	0.674699	1.358356	0.731707	1.390185	0.505882
3	1.255809	0.768293	1.293919	0.60241	1.293692	0.623529
4	1.351289	0.571429	1.368893	0.658537	1.348776	0.535714
5	1.33272	0.578313	1.382775	0.595238	1.402478	0.481928
6	1.33142	0.654762	1.332977	0.646341	1.356943	0.547619
7	1.314666	0.662651	1.359642	0.573171	1.408428	0.529412
8	1.368511	0.470588	1.394069	0.419753	1.390349	0.488095
9	1.24727	0.788235	1.314117	0.777778	1.338868	0.559524
10	1.283623	0.8	1.344933	0.654762	1.422905	0.592593
11	1.20191	0.452381	1.157062	0.53012	1.013648	0.590361
12	1.224905	0.928571	1.216668	0.75	1.222453	0.646341
13	1.185058	0.785714	1.247974	0.518519	1.278627	0.517647
14	1.527378	0.470588	1.488601	0.512195	1.542603	0.590361
15	1.208429	0.60241	1.255718	0.573171	1.317728	0.376471
16	1.210407	0.529412	1.30498	0.518072	1.31457	0.47561
17	1.234181	0.662651	1.292194	0.607143	1.247807	0.39759
18	1.261804	0.670588	1.31725	0.679012	1.383627	0.678571
19	1.26245	0.583333	1.31122	0.559524	1.337607	0.585366
20	1.33761	0.576471	1.40143	0.560976	1.436592	0.518072
21	1.277687	0.630952	1.322724	0.578313	1.344591	0.481928

Table 4.2. Accuracy and RTs for Two, Four, or Eight items for change detection task per participant for *Experiment 3b*.

Behavioral Results:

Analysis of the RT data did not reveal any significant effect for either RT or response accuracy as a function of VWM (see Figure 4.7) in the 50/50 experiment.

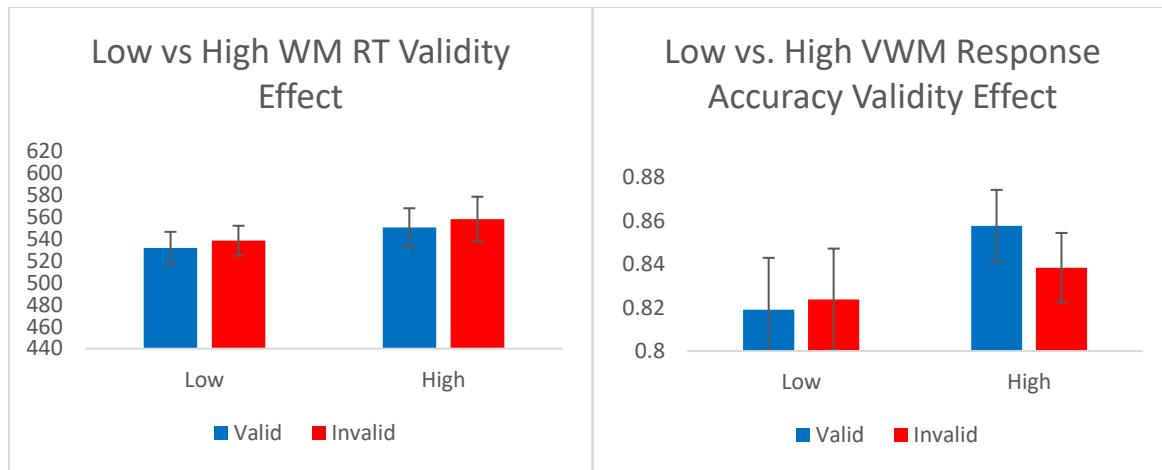


Figure 4.7 (left) RT and (right) Accuracy for the Validity effect for low vs. high VWM in Experiment 3b.

Eye-Tracking

Rate, amplitude and direction Experiment 3b

There were no differences in rate, amplitude or direction in this experiment either in the main omnibus ANOVA or the separate follow-ups run on the two VWM groups separately (all p 's > .09 – see Figure 4.8 and 4.9).

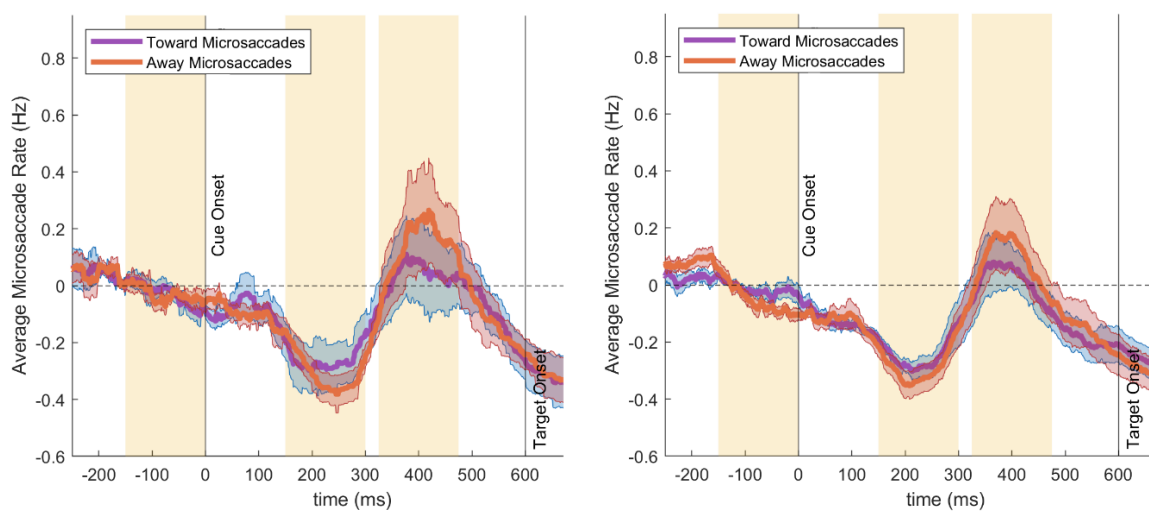


Figure 4.8 (left) cue MS rate for the High-VWM group (right) low-VWM group of Experiment 3b.

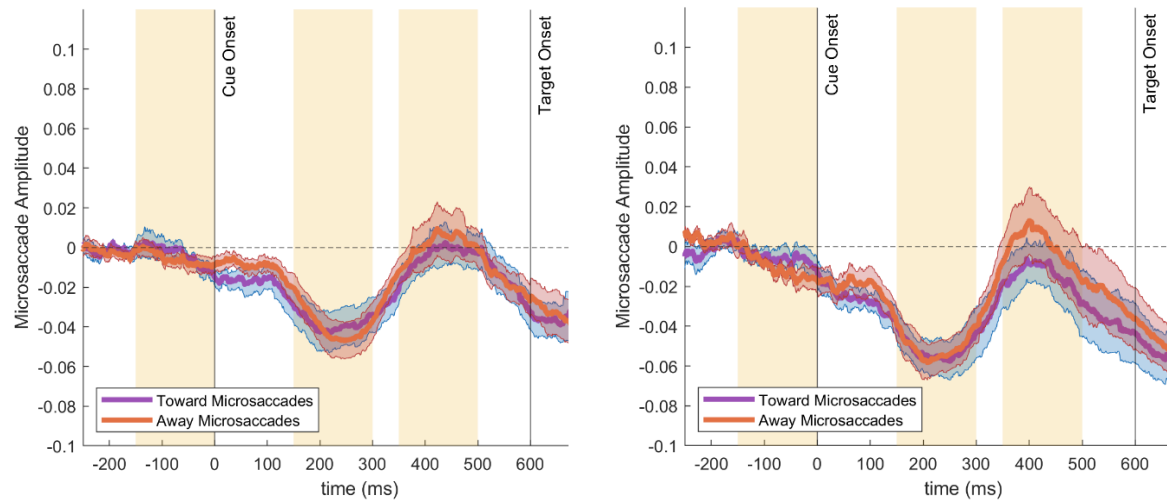


Figure 4.9 (left) cue MS amplitude for the High-VWM group (right) low-VWM group of Experiment 3b.

ERPs to targets:

Plotted in Figures 4.10 are the difference wave ERPs contrasting the Validity effect for the three MStypes in Experiment 3b. The top panel is for the High WM group, and the bottom panel is for the Low WM group. There were no differences in the Validity effect on any of the ERP components (C1, P1 or N1) as a function of VWM either in the overall analysis or when comparing Validity effects separately for the three types of MSs (all p s > .1).

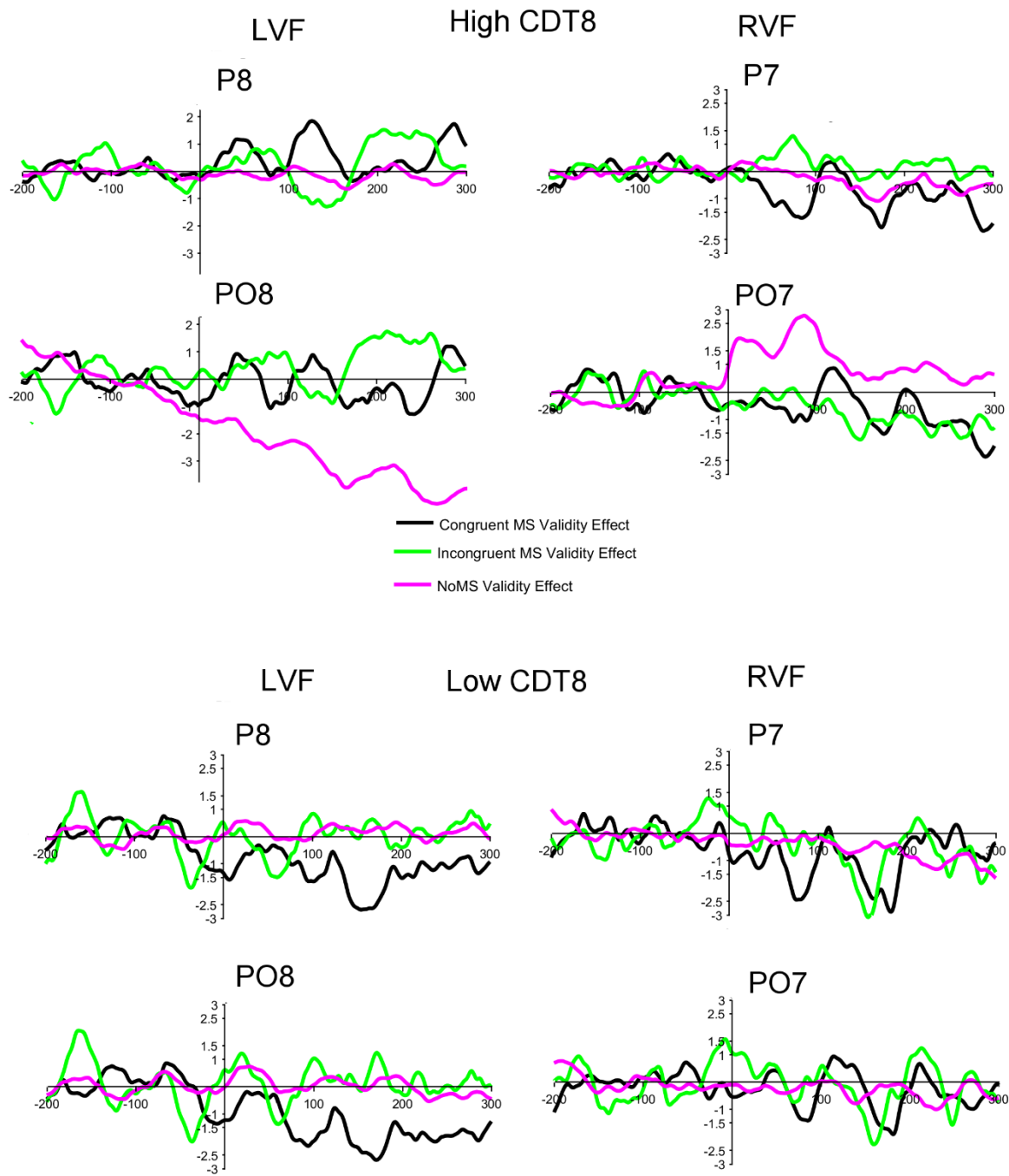


Figure 4.10. Validity effect difference waves for each MSType for the High (top) vs. Low (bottom) VWM groups in the 50/50 experiment (3b).

Exploratory analyses:

While there were no differences on any of the measures as a function of VWM capacity and cue-predictiveness (Experiment 3a compared to Experiment 3b), exploratory analyses collapsing the two experiments did reveal differences between High- and Low-VWM groups.

There was a marginal difference in the Validity effect difference waves for congruent MSs as a function of VWM group ($F(1,38) = 3.9$, $p = 0.055$) with low-VWM subjects showing a larger C1s (see Figure 4.11). There were no VWM effects for the Incongruent or No MS comparisons ($ps > .3$).

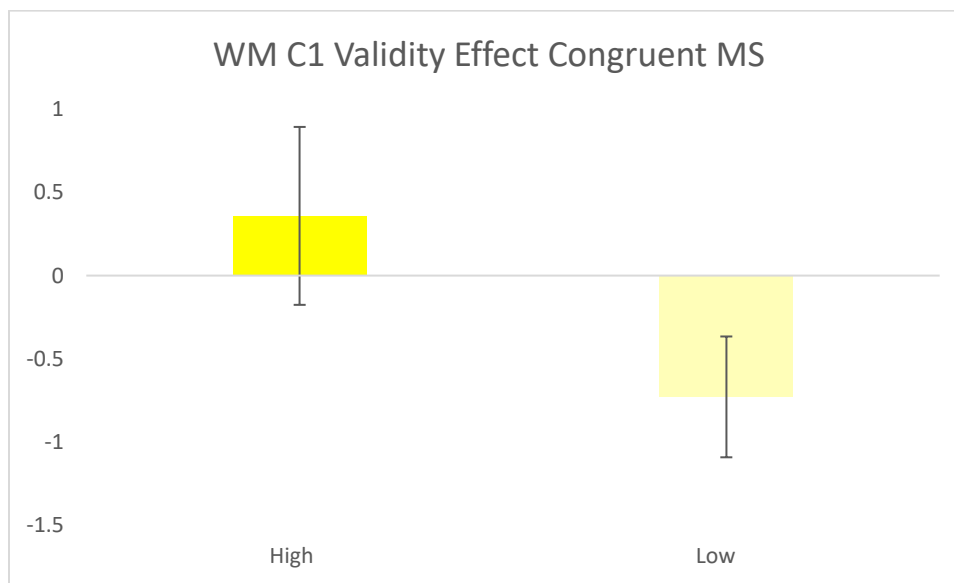


Figure 4.11. C1 attention effects for the High- and Low-VWM groups collapsed across both Experiments (3a and b) following congruent MSs.

As can be seen in the Figure 4.12 for the P1 there was a significant VWM (main effect of VWM: $F(1,38) = 6.21$, $p = 0.02$) validity effect for congruent MSs but there were no comparable effects for the incongruent and No MS conditions ($ps > .38$). The P1 congruent MS validity effect was larger for High- compared to Low-VWM participants.

There were no N1 validity effect differences as a function of Experiment (all $ps > .06$).

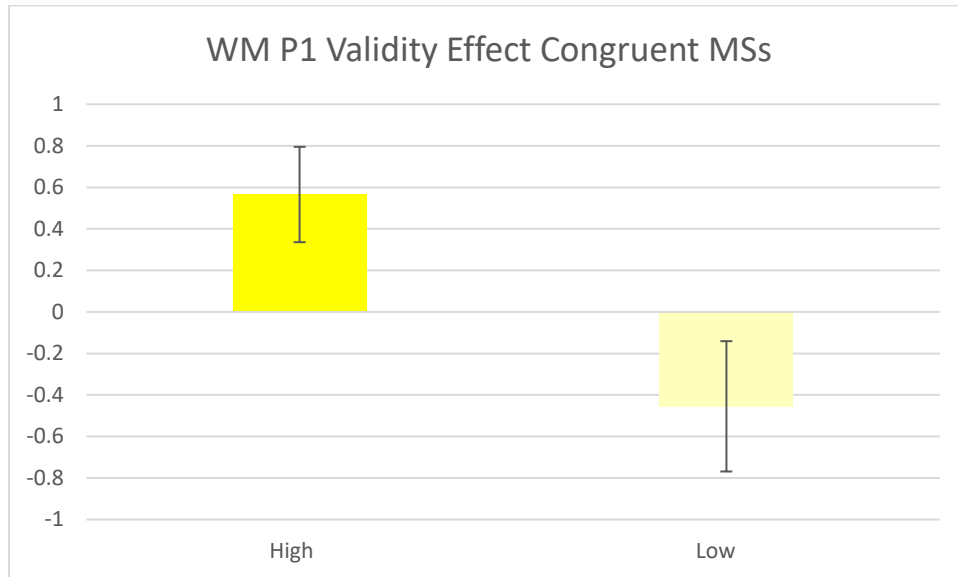


Figure 4.12. P1 attention effects for the High- and Low-VWM groups collapsed across both Experiments (3a and b) for congruent MSs.

Discussion

Experiment 3a: Contrary to the original hypotheses, no significant Validity x VWM group interactions for either accuracy or RT were observed. However, because of planned comparisons, and in line with the original hypotheses, the High-VWM group was significantly faster at responding to valid compared to invalid trials, while no difference was observed for the Low-VWM participants. Interestingly, for congruent-MS trials, High-VWM participants were significantly faster on valid compared to invalid trials, while no effects were observed in the Low-VWM group. Likewise, the MStype x VWM group interaction was not significant for MS rate data, but as with the other dependent measure, planned comparisons were explored. For the High VWM group, MS rate was significantly greater for congruent MS compared to incongruent ones, and more MSs were made towards compared to away from the cue, while no such patterns were observed in the Low group. Conversely, while there was no significant MStype x VWM group interaction for MS amplitude, planned follow-up comparisons did not reveal any

differences for either the High- or Low-VWM groups. Contrary to the original hypotheses, the C1 component did not differ between High- and Low-VWM groups in Experiment 3a. However, for this experiment the High-VWM group did produce significantly greater P1 mean amplitude on valid trials compared to invalid trials when the electrodes were contralateral to the visual field of the target. There were no comparable differences observed for the Low-VWM group. The same pattern was observed for the N1 epoch, where High-VWM participants produced a more negative N1 on valid trials contralateral to the target side compared to invalid trials, while no effects were observed for the incongruent or no MS conditions.

Experiment 3b: No significant differences between VWM groups were observed for either MS rate or amplitude, at the omnibus level or in follow-up planned comparisons. There were no differences of validity on any of the ERP components (C1, P1 or N1) as a function of VWM either in the overall analysis when comparing validity effects separately for the three types of MSs.

Exploratory analyses: While there were no differences on any of the measures as a function of VWM capacity and cue-predictiveness (Experiment 3a compared to Experiment 3b), exploratory analyses including all 41 participants by collapsing the two experiments did reveal some different patterns in the two VWM groups. Unexpectedly, for congruent microsaccades, Low-VWM participants showed a greater C1 attention effect (valid minus invalid) compared to the High-VWM group. However, the opposite pattern was observed for the P1 epoch, where High-VWM participants produced a larger P1 attention effect compared to the Low-VWM group. No experiment differences were observed for the N1 epoch, and similarly no differences at any of the measured time-windows (C1, P1, N1) were observed for incongruent or no MS conditions.

Chapter 5: General Discussion

Here, the relationship between covert spatial attention and microsaccades was investigated in a series of experiments. **For each chapter, the experiments were split by the predictiveness of the cue, either a) 80/20 validity or b) 50/50 validity.** In Chapter 2, the rate, amplitude, and direction of microsaccades were examined as a function of the predictiveness of endogenous cues. Chapter 3 specifically addressed the neurophysiological correlates of early visual attention (C1, P1, N1 ERPs) and target-related alpha power as a function of whether a microsaccade was made towards (congruent) or away (incongruent) from the subsequent target, or when no microsaccade was made. Lastly, Chapter 4 asked whether visual working memory differences systematically modulate microsaccade associated attention effects. Crucially, the present findings **hint at a possible link between congruent microsaccades and enhanced attention, as evidenced by improvements in reaction times, ERP components (P1, N1), and target alpha power, in addition to weak evidence of attention effects within the domain of visual working memory.** On the other hand, these same measures following incongruent and no microsaccades did not show similar patterns.

A link between covert spatial attention and microsaccades—small fixational eye movements once considered stochastic noise—is rooted in the framework of the Premotor Theory of Attention, in which a shift of attention is functionally equivalent to a motor program for a saccade (Basso & Wurtz, 1998; Rizzolatti et al., 1987; White & Munoz, 2011). Consistent with this, microsaccades are now thought to index the locus of covert attention, evidenced by the observation that more microsaccades are made towards compared to away from an instructional, predictive cue (Engbert & Kliegl, 2003; Hafed & Clark, 2002). This behavioral coupling is supported by neurophysiological evidence that the SC and FEF, structures intrinsic to saccade

generation, are also causally involved in the control of covert spatial attention (Moore & Fallah, 2001; Müller et al., 2005). Specifically, the rostral SC contains a topographic representation of foveal space where neurons exhibit burst activity preceding microsaccades that is functionally indistinguishable from the activity driving larger saccades (Hafed et al., 2009; Hafed & Krauzlis, 2012). Furthermore, neurons specific to different functions have been identified in both SC and FEF; visual neurons, motor neurons, and visuomotor neurons (Cohen et al., 2009; Hafed et al., 2021). One possibility is that these visuomotor neurons subserve this attention-oculomotor association. Consequently, top-down attentional signals that potentiate specific coordinates within this shared oculomotor map result in a directional bias of microsaccades toward the attended location (Hafed & Clark, 2002; Yuval-Greenberg et al., 2014). Moreover, this relationship appears to be functional rather than epiphenomenal; recent evidence indicates that the attentional modulation of neural firing rates in extrastriate cortex (e.g., Area V4) is selectively enhanced following microsaccades directed toward the attended stimulus, suggesting a mechanism for rhythmic sampling and sensory refreshing (Lowet et al., 2018; Srinivasan et al., 2025).

Separately, there has been a debate as to how early top-down processes of attention can affect the feed-forward signals of visual information (see special issue in *Cognitive Neuroscience*, 2018, edited by Slotnick), despite the fact that there seems to be feedback attentional signals from higher-order visual areas that do indeed affect primary visual cortex (Di Russo et al., 2002). While there has been some evidence that attention can act as early as the lateral geniculate nucleus (Briggs, Mangun, & Usrey, 2013), whether these signals can influence information processing at V1 has been a matter of contention. Also, there is additional evidence for attentional effects at this earliest visual area (Bouhnik, Korch, & Slovlin, 2025; Kelly et al.,

2008), but the majority view is that the earliest attention acts first in extrastriate areas (Mangun, 1995; Mangun & Hillyard, 1991; see special issue in *Cognitive Neuroscience*, 2018, edited by Slotnick).

The studies in this dissertation attempted to further explore the relationship between attention in early visual areas and the role of microsaccades. In Experiments 1a and 1b, the effect of cue-predictiveness on microsaccade rate, amplitude, and direction was examined by manipulating the probability that a cue would indicate the target side (Experiment 1a: 80/20 valid/invalid; Experiment 1b: 50/50 valid/invalid). Overall, microsaccades exhibited the classic pattern (Engbert & Kliegl, 2003) of an initial decrease in microsaccade rate followed by a rebound period and then return to baseline. While the current study found differences in microsaccade rate during the rebound period in the 80/20 experiment (more eye-movements towards compared to away from the direction of the cue), no such differences were observed in the 50/50 condition. This is contrary to findings reported by Lv et al. (2022) where microsaccade rate differences were observed for 50/50, 75/25, and 100% cueing conditions. However, they reported more microsaccades being made *away* from the cue direction, whereas the current results in the 80/20 condition reported an increased rate for microsaccades made towards. One reason for this discrepancy may be due to the differences in experimental design, where the previous study confounds endogenous and exogenous attention. Specifically, Lv et al. (2022) utilized peripheral cues and thus may have a stronger IOR effect than the current studies. The previous authors also did not utilize a gaze-contingent presentation of stimuli (targets), and the procedure in the current study incorrectly informed participants that the cue indicated the most likely side of the target (although the participants did not appear to use the cue given behavioral and other electrophysiological measures), all of which may have contributed to the differences.

Importantly, the overall rate of microsaccades was greater when cues predicted the subsequent target (80/20) compared to when they did not (50/50), contrary to other findings, possibly suggesting that microsaccade rate may be more deterministic than previously thought (Liu et al., 2023). This divergence in findings again could possibly be explained by differences in task design, as Liu et al. (2023) required participants to hold items in working memory and retroactively cued them to attend to one of two items, whereas the current task cued participants to subsequent targets.

The results of microsaccade amplitude differences when a microsaccade is directed towards compared to away from the cue in the current experiments is in line with prior findings (Lv et al., 2022). However, like rate, this was in the opposite direction as the current findings, as they reported less amplitude for microsaccades made towards compared to away from the cue, again possibly due to the differences in exogenous and endogenous attention.

In Experiments 2a and b, the overarching goal was to investigate whether microsaccades were associated with facilitated attentional processes as some researchers have suggested (Bouhnik, Korch, & Slovin, 2025; Kelly et al., 2008, Lowet et al., 2018; Srinivasan et al., 2025). An important observation here is that microsaccades did not appear to be systematically related to the earliest visual ERP component, C1. Specifically, in the 80/20 experiment congruent microsaccades were not associated with a larger attentional effect (valid minus invalid) for the C1 component compared to incongruent or no microsaccade conditions, contrary to the original hypotheses. Surprisingly, congruent microsaccades were associated with greater C1 validity effects in the 50/50 experiment, when the validity of the cue was nonpredictive (see below for further discussion of this finding). One important thing to note here is that one prior study that greatly influenced this current work took into consideration individual differences in primary

visual cortex morphology (Kelly et al., 2008). Specifically, stimulus positions were varied based on which diagonal set resulted in the largest C1 component for a given individual, while the current study held the stimuli positions constant across participants. Thus, this could account for why Kelly and colleagues (2008) found a more robust C1 ERP and why no such attention effects were observed in the current studies (see special issue in *Cognitive Neuroscience*, 2018, edited by Slotnick). Furthermore, Wolf and colleagues (2022) demonstrated that subtle, systematic deviations in eye position toward the attended location can artificially inflate C1 amplitudes due to retinotopic sensitivity. When these gaze deviations were statistically controlled, C1 attention effects disappeared or were reversed (Wolf et al., 2022). The current study employed a gaze-contingent stimuli design, in which eye movements made prior to the presentation of targets would reposition the stimuli in real-time in order to control for retinal eccentricity confounds, which Kelly and colleagues (2008) did not do.

The failure to see C1 attention effects somewhat contrasts with the finding that congruent microsaccades were associated with greater P1 attention effects and importantly the incongruent or no microsaccade conditions did not show similar effects. Specifically, there was a greater validity effect (valid minus invalid) at electrodes contralateral to the target side following congruent microsaccades, which suggests that microsaccades are possibly associated with facilitated attention in extrastriate areas (Di Russo et al., 2002; Lowet et al., 2018; Mangun, 1995; Mangun & Hillyard, 1991). While the omnibus test indicated that this attention effect did not differ significantly as a function of MStype, the planned comparisons suggest there may be interesting differences between congruent and incongruent/no ms conditions. To further interrogate these findings, future studies may attempt to increase the number of microsaccades, specifically on invalid trials, to increase statistical power. This idea is supported by evidence in

non-human primates -- as previously described, Lowet and colleagues (2018) demonstrated that when a microsaccade toward the upcoming target was made, V4 neurons in the receptive field had increased firing rates compared to the neurons outside of that receptive field. But when a microsaccade was directed *away* from the upcoming target, no attentional modulation was observed for V4 firing rates. Similarly, microsaccades toward an attended stimulus significantly enhance object representations and sharpen tuning curves in V4 (Srinivasan et al., 2025).

A note about the canonical P1 attention effect observed in Experiment 2a is that it was not as robust as one might expect (Mangun, 1995; Mangun & Hillyard, 1991). One possibility for this is that as previously described, the task used here employed a gaze-contingent presentation of stimuli, which updates stimuli locations in real-time if a microsaccade was made just before the targets were presented. One possible reason for the relatively weakened P1 attention effect could be that the extrastriate areas (particularly V3A) that contribute to the P1 (Clark & Hillyard, 1996) are used to predict future locations based on a planned saccade (Nakamura & Colby, 2002). If these extrastriate areas predict the landing location of a saccade (in this case a microsaccade) in retinal coordinates, but by the time the saccade has landed on its final location and the stimulus has moved, then there may be a mismatch between the predicted and actual location and thus a weakened or absent attentional state. Likewise, Guzhang, Shelchkova, Clark and Poletti (2023) found evidence that microsaccades may enhance attention at a very fine resolution (10 arcminutes). Specifically, the study revealed a spatially localized enhancement of visual sensitivity at the precise future landing site of the microsaccade, which again may point to an unintended confound in the current study.

Adding to the conundrum, under the above line of thinking one would expect a robust P1 attention effect on trials with no microsaccades, which was not apparent in the current data. One

thing to consider here is that this task employed a variable CTI of 400-800 ms (mean of 600), so one possibility for this lack of P1 attention effect on no MS trials is that they happened to fall on the shorter side of this range, not leaving enough time for a full-blown attention effect. This possibility might also have contributed to the absence of microsaccades in this condition (i.e., less overall time allowing for such an eye movement). Future analyses could investigate whether any such relationship exists, and/or future studies could use a fixed CTI to avoid this potential confound.

In Experiment 2a following a congruent microsaccade contralateral alpha power was observed to be significantly reduced (desynchronization) on valid compared to invalid trials, aligning with the original hypotheses. This pattern was not observed for incongruent or no MS trials, further indicating the unique association of congruent microsaccades with spatial attention effects. Importantly, this pattern was not observed for Experiment 2b, where, and if anything, the relationship was reversed (greater contralateral alpha power desync for invalid trials compared to valid trials). This finding adds further tentative support to the coupling of the attentional and oculomotor systems (i.e., Premotor Theory of Attention). However, while the omnibus test failed to reveal significant differences in the attention effect as a function of MSType, the planned comparisons do suggest there may be interesting differences between congruent and incongruent/no MS conditions. To further interrogate these findings, future studies may attempt to increase the number of microsaccades, specifically on invalid trials, to increase statistical power. Given that alpha power is inversely related to visual cortical excitability (the gating by inhibition hypothesis; Jensen & Mazaheri, 2010), the pronounced desynchronization on valid, congruent-microsaccade trials may reflect a heightened attentional state when both top-down cognitive cues and bottom-up oculomotor preparation align at the target location. While previous

studies have reported similar findings to spontaneous microsaccades (Liu et al., 2022), the current study extends this to attention-directed microsaccades.

Interestingly, the current study did not observe an alpha lateralization when no microsaccades were made, as was previously reported (Liu et al., 2023). One possible reason for this discrepancy could be due to task requirements; previous studies that induced alpha lateralization on no MS trials instructed participants to memorize two colored bars and employed a retro-cue to manipulate attention (Liu et al., 2022), which may have resulted in their observation. Another possibility is the one mentioned above; the no MS trials might have disproportionately been the short CTI trials, therefore not leaving enough time for target alpha effects.

Contrary to the original hypotheses, no microsaccade-related benefits to behavior were observed, and in fact participants responded *slower* to the targets following congruent microsaccades in Experiment 2b. One reason for this may be that Srinivasan, Lowet, Gomes, and Desimone (2025) found RT benefits when the last microsaccade before the target was made towards versus away from the upcoming stimulus, which may point to the idea that instead of analyzing the first microsaccade (as some others have done; Denison et al., 2019; Laubrock et al., 2010; Liu et al., 2022; Tian et al., 2016), it may be more beneficial to look at the last MS. However these may often be made away, as a second part (or returning) of the initial “towards” microsaccade.

Surprisingly, in Experiment 2b there was a significant effect of validity for the C1 component (a larger C1 for valid compared to invalid trials following congruent microsaccades). Given that cues did not predict the upcoming target location, and thus there was no reason for participants to systematically attend to them (supported by the lack of attention-related behavior

and P1 component effects), it is curious that such an observation on the earliest visually-evoked component was seen. One possible reason for this could be that given this study did not present stimuli in a way to maximize the C1 component on an individual basis as previous research has done (Kelly et al., 2008), it is possible that by chance participants in this experiment had a V1 morphology more suited to the pre-fixed locations of the target stimuli, and because the C1 was more robust for each individual on average (compared to Experiment 2a), an attentional difference was observed. However, this does not necessarily answer why an attentional difference was observed despite a lack of behavior and other canonical signatures of attention (P1/N1), so this may need to be investigated further in the future.

In Experiment 3a, while there was no significant interaction of MStype and VWM group for MS rate or amplitude, planned follow-ups suggested VWM capacity may be associated with differences in eye-movements. Specifically, MS rate was significantly greater for congruent compared to incongruent MS in High-VWM individuals, while no difference was observed in the Low group. This, along with the finding that no similar pattern was observed in Experiment 3b where attention was not preferentially deployed as a function of the cue, suggests a possible difference which merits further exploration in the future. Individual differences in VWM did not result in attentional effects for the C1 component (but see discussion of the exploratory analyses below), contrary to the original hypotheses. These results further support the majority view; the earliest visual component (likely to arise in V1) seems to be immune to modulations of attention in a feed-forward manner (see special issue in *Cognitive Neuroscience*, 2018, edited by Slotnick). While the omnibus test indicated that there was not a significant validity by VWM interaction, the planned comparisons suggest there may be interesting differences here. Specifically, on congruent microsaccade trials, High-VWM individuals exhibited greater P1 and

N1 mean amplitude differences between valid and invalid trials, while Low-VWM individuals showed no such difference. To further interrogate these findings, future studies may attempt to increase statistical power by including more participants per group, as in the current studies the N per VWM group (~10) was relatively low. Together these findings provide some support for the hypothesis that working memory capacity relies on the efficiency of early top-down sensory gating (Zanto & Gazzaley, 2009). This finding aligns with research demonstrating that the ability to modulate early visual processing (specifically the P1 and N1 components) is a critical predictor of subsequent working memory performance; high-performing individuals significantly modulate these components to enhance relevant and suppress irrelevant information, whereas low-performing individuals fail to differentially modulate neural activity based on attentional relevance (Zanto & Gazzaley, 2009). Furthermore, the magnitude of this early P1 attentional modulation (roughly 100 ms post-stimulus) has been shown to correlate directly with recognition accuracy, suggesting that High-VWM individuals utilize superior executive control to sharpen the fidelity of sensory representations during the initial encoding phase (Rutman, Clapp, Chadick, and Gazzaley, 2010).

The lack of a significant P1 and N1 modulation in the Low-VWM group, while not providing strong evidence, is nevertheless consistent with the possibility of a failure or weakness in sensory gain control, a mechanism thought to amplify neural signals in extrastriate cortex for validly cued locations (Hillyard, Vogel, & Luck, 1998). This deficit is consistent with the filtering efficiency account, which posits that low-capacity individuals possess porous attentional filters that allow irrelevant or invalidly cued information to be processed to the same extent as targets, thereby consuming limited storage resources (Fukuda & Vogel, 2009; Vogel, McCollough, & Machizawa, 2005). Conversely, the High-VWM group's robust N1 modulation

reflects a successful discrimination process within the focus of attention, confirming that higher capacity is associated with the ability to maintain a precise and exclusive attentional set that resists capture by invalid spatial locations (Gaspar et al., 2016; Vogel & Luck, 2000). Ultimately, these electrophysiological patterns suggest that the behavioral advantage of the High-VWM group stems from their ability to implement early selection (gating) in the visual cortex, minimizing the processing resources to invalid locations that characterizes the Low-VWM group (Gaspar et al., 2016; Zanto & Gazzaley, 2009).

One final result that deserves further discussion is the finding in the VWM exploratory analyses comparing the ERPs across the two experiments. In these comparisons there was an attentional effect on the C1 as a function of VWM group following congruent MSs. However, it was the low-VWM participants who tended to show a C1 attention effect (i.e., greater negativity for valid than invalid targets) while the high-VWM group actually exhibited a reversed C1 (i.e., larger positivity for valid than invalid trials). Given the discussion above about the role of VWM on spatial attention this finding is curious. One possibility for this pattern could be that what looks like a reversed C1 effect in the high-VWM group is actually the later P1 attention effect starting earlier than is typical for this group, which would present as an apparent reversal of the C1. A future study might attempt to resolve this apparent contradictory pattern by looking at a larger sample of participants and using continuous measures of VWM (as opposed to median splits) to further explore individual differences in early ERP measures of spatial attention.

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Appendix

The following two tables show the number of trials that went into the ERP averages per participant for both Experiments 2a and b.

Experiment 2a:

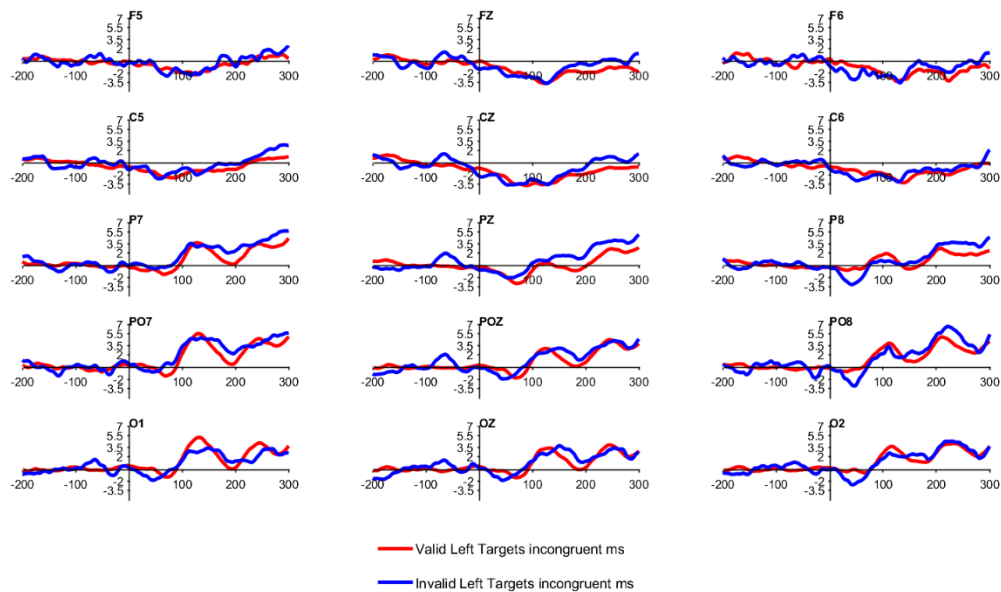
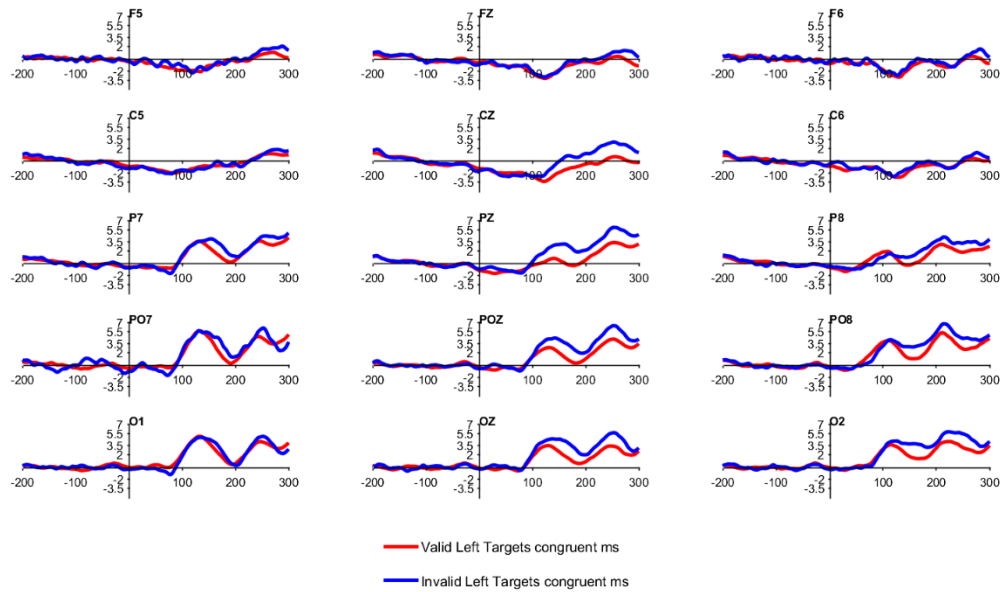
subID	valid	invalid	cong ms	incong ms	no ms	left	right
1	733	184	264	267	386	460	457
2	517	124	190	145	306	273	368
3	680	159	80	57	702	403	436
4	579	141	137	103	480	338	382
5	617	156	312	135	326	407	366
6	608	134	151	150	441	367	375
7	684	168	147	116	589	432	420
8	732	183	164	97	654	459	456
9	749	189	83	40	815	482	456
10	703	171	58	29	787	422	452
11	655	168	401	121	301	383	440
12	746	182	64	21	843	445	483
13	587	148	242	235	258	336	399
14	740	182	505	291	126	455	467
15	619	146	246	210	309	401	364
16	671	173	120	87	637	376	468
17	706	178	264	202	418	475	409
18	688	174	313	91	458	421	441
19	638	145	474	218	91	411	372
20	664	173	196	81	560	427	410
mean	665.8	163.9	220.55	134.8	474.35	408.65	421.05

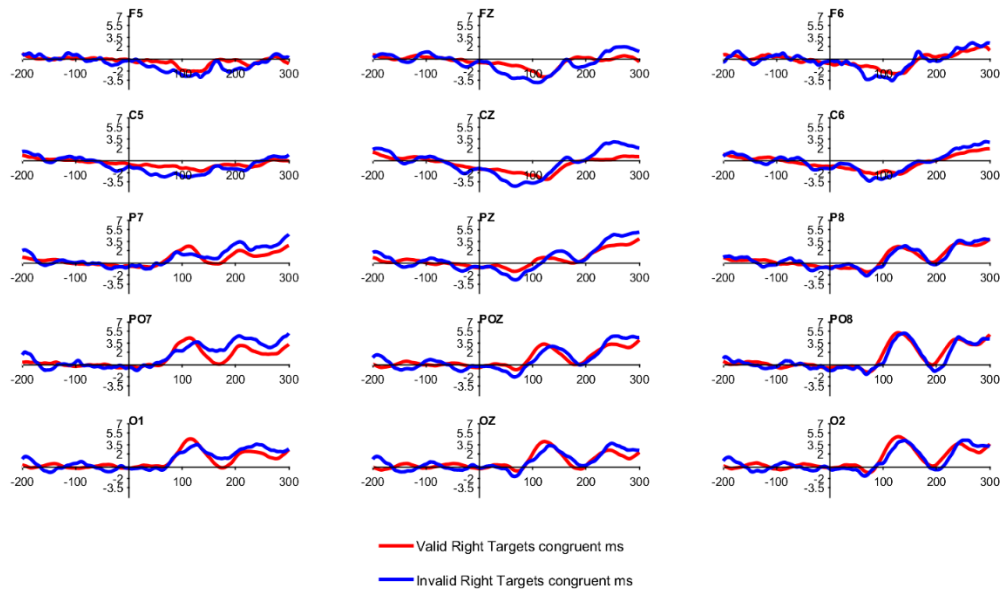
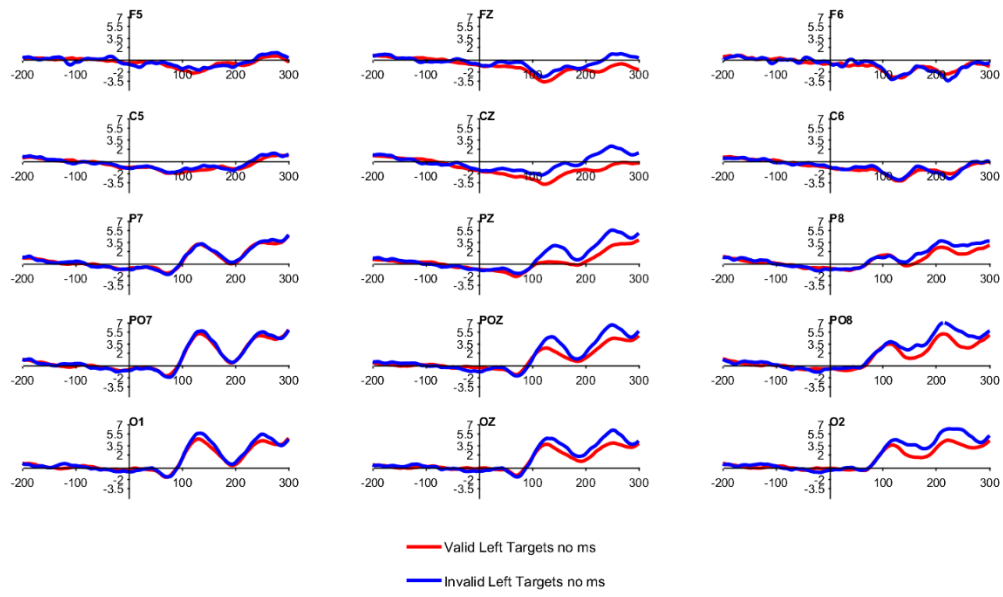
Experiment 2b:

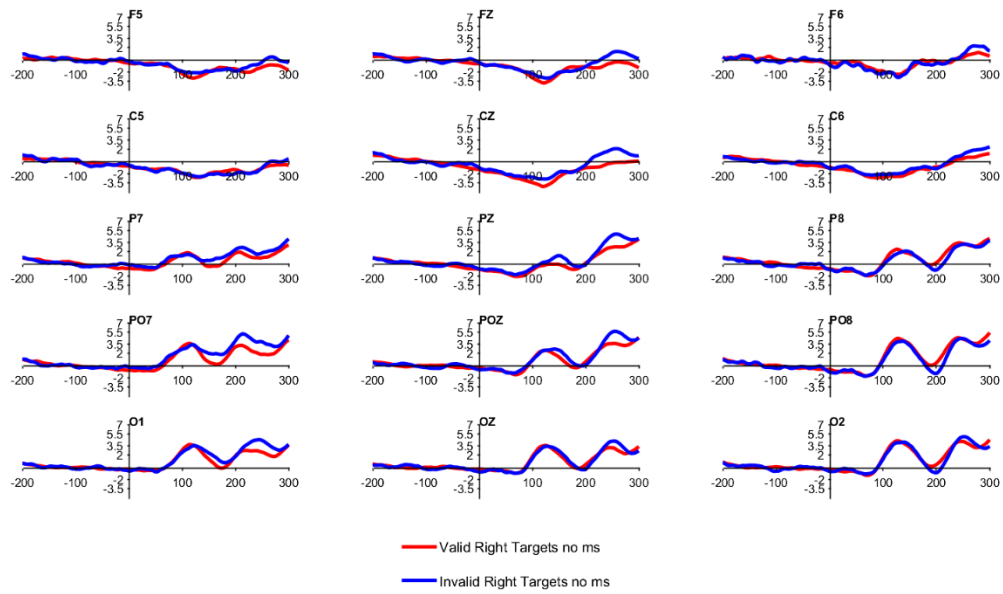
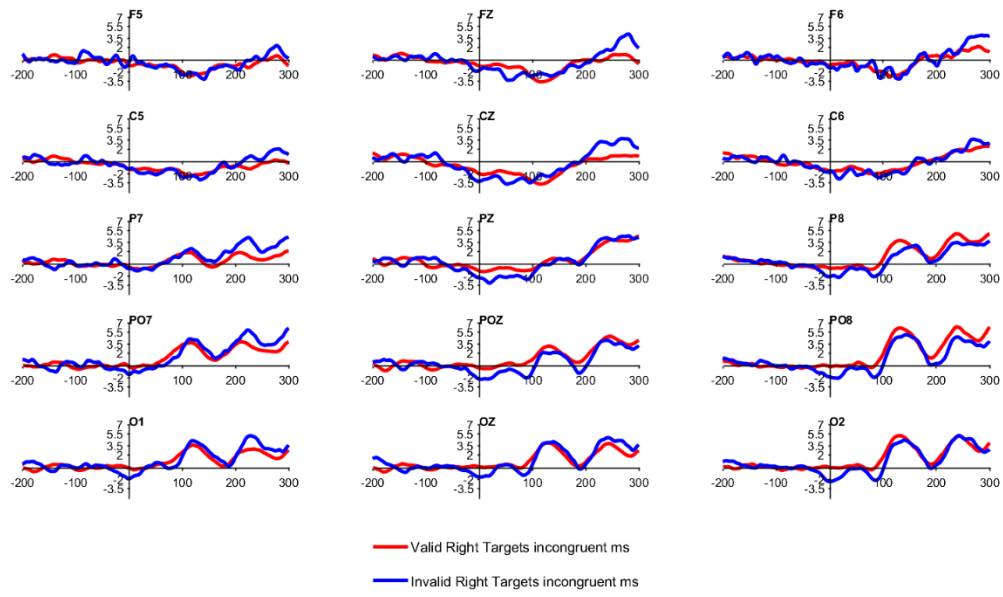
subID	valid	invalid	cong ms	incong ms	no ms	left	right
1	406	366	30	42	700	362	410
2	461	433	87	123	684	455	439
3	398	416	43	43	728	400	414
4	367	352	268	166	285	350	369
5	233	253	73	16	397	229	257
6	381	428	122	134	553	423	386
7	400	405	86	69	650	390	415
8	383	395	124	115	539	417	361
9	375	406	210	230	341	386	395
10	440	487	157	109	661	462	465
11	413	377	132	65	593	354	436
12	456	478	143	130	661	471	463
13	366	358	40	34	650	362	362
14	357	309	127	81	458	333	333
15	450	461	255	236	420	468	443
16	410	416	140	54	632	397	429
17	442	458	248	173	479	446	454
18	456	428	218	194	472	435	449
19	353	358	58	84	569	342	369
20	328	334	125	142	395	321	341
21	394	364	184	163	411	414	344
22	409	408	203	200	414	390	427
mean	394.4545	395	139.6818	118.31818	531.45455	391.2272727	398.2272727

Plotted in the 12 Figures below are the ERPs from the 12 critical bins used to analyzed the data in Experiments 3a and 3b. Each plot shows the validity contrast to targets presented in one visual field (left and right) for each of the three types of microsaccades.

Experiment 3a:







Experiment 3b:

