MAGNOCELLULAR AND PARVOCELLULAR INFLUENCES ON REFLEXIVE ATTENTION

Anthony J. Ries

A dissertation submitted to the faculty of the University of North Carolina at Chapel Hill in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Department of Psychology (Cognitive Psychology).

Chapel Hill
2007

Approved by

Advisor: Joseph Hopfinger, Ph.D.
Reader: Aysenil Belger, Ph.D.
Reader: Kelly Giovanello, Ph.D.
Reader: Mark Hollins, Ph.D.
Reader: Neil Mulligan, Ph.D.
Reader: Gordon Pitz, Ph.D

ABSTRACT

ANTHONY RIES: Magnocellular and Parvocellular Influences on Reflexive Attention
(Under the direction of Joseph Hopfinger, Ph.D.)

There is currently disagreement in the visual attention literature regarding the stimulus features capable of triggering a reflexive shift of attention. One theory posits that features activating the magnocellular (M) visual stream, such as abruptly appearing objects with luminance contrast and low spatial frequencies, are responsible for activating the reflexive attention system (e.g. Steinman et al., 1997; Yantis and Egeth, 1997). However, recent experiments suggest stimuli activating the parvocellular (P) stream, such as isoluminant colors with high spatial frequencies, may be equally important for initiating reflexive shifts of attention (e.g. Lu, 2006; Yeshurun, 2004). Using behavioral and event-related potential (ERP) measures, we designed stimuli to stimulate either the M or P system to test whether the predominate activation of these systems trigger similar reflexive attention mechanisms, or if mechanisms of attentional capture are engaged differently depending on M or P activation. We predicted that similar attention effects would be observed if both pathways triggered automatic attentional orienting. However, if only magnocellular activation engages the reflexive attention system then we hypothesized that attention effects would only be seen when stimuli activated this system and not the P system. The present findings support the view that both systems are capable of triggering reflexive visual orienting. Specifically, reaction times (RTs) to target stimuli were speeded and the P1 and

P300 components enhanced when spatially preceded by both M and P cues at short inter-stimulus intervals (ISI's), but these findings were characteristically different at long ISIs where inhibition of return (IOR) typically occurs. Further evidence supporting attention capture from M and P activation was evidenced by a greater negativity to uncued compared to cued trials at short ISIs, i.e. the IIN component. However, we also found evidence that M and P stimulation produced different effects depending on whether the target stimulus activated the M or P system. Together these results are consistent with the basic processing characteristics of the M and P pathways and show that activation either pathway can trigger a reflexive shift of visual attention.

ACKNOWLEDGEMENTS

I would like to express gratitude to my advisor Dr. Joe Hopfinger for his guidance, support, and encouragement throughout the course of my graduate training. I would further like to thank the following individuals for their contributions to this dissertation and participation on my dissertation committee: Dr. Aysenil Belger, Dr. Kelly Giovanello, Dr. Mark Hollins, Dr. Neil Mulligan and Dr. Gordon Pitz. I am also indebted to my wife, Dr. Angela Poppe Ries, my family, friends and pets for their support, love, and understanding throughout my matriculation at the University of North Carolina in Chapel Hill.

TABLE OF CONTENTS

Page

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

As we navigate through our environment we are only able to process a fraction of the available information due to a limited pool of processing resources available to our visual system. Therefore, our visual system has evolved attentional mechanisms to select and process the most relevant stimuli and inhibit unimportant or distracting information (Desimone & Duncan, 1995; Luck et al., 1997; Posner, 1980). Mechanisms of attention enable us to focus on what we want to see or what is important to us instead of everything available to see. Selecting information through mechanisms of attention enhances perception (Carasco et al., 2004) and action (Tipper, 2004) as well as increases the likelihood that attended information is retained in memory (Hollingworth, Williams, and Henderson, 2001).

Two processing mechanisms in the brain govern the selection of relevant visual information. The first mechanism is influenced by the intrinsic properties of the visual stimuli such as luminance, color, and orientation. This is commonly referred to as bottom-up processing and is directly involved in triggering reflexive shifts of attention. Unlike the first, the second mechanism reflects the willful intentions, goals, or memories of the observer; this is reflective of top-down processing. The Biased Competition model (Desimone and Duncan, 1995) contends that these two mechanisms interact and compete for the limited supply of processing resources in the brain. In other words, competition for the limited supply of attentional resources is directly influenced by the relative contribution of external visual features and the internal state of the observer. The winner of this competition receives

preferential processing compared to other competing stimuli within the visual field by gaining further access to memory and motor systems (Kastner and Ungerleider, 2000).

In some cases highly salient stimuli will 'pop out' and win the competition for processing resources and automatically attract attention through their inherent physical properties with little influence from top-down mechanisms. This is most commonly referred to as attentional capture. For example, a sudden flash of lightning or the sudden movement of a deer on the side of the road will automatically attract attention without any volitional effort from the observer. Such events with high feature salience, like an abruptly appearing object (Jonides, 1981, Yantis and Jonides, 1984; Yantis and Hillstrom, 1994;), an abrupt luminance change (Posner, 1980; Atchley, Hillstrom and Kramer, 2000; Snowden, 2002; Theeuwes, 1995), or the onset of motion (Abrhams, 2004; Folk and Remington, 1994) have reliably demonstrated their ability to reflexively capture attention.

Behavioral Correlates of Attentional Capture

One of the most widely used paradigms used to assess attentional capture comes from Posner and Cohen (1984). In their seminal study, they employed an exogenous spatial cueing experiment to study reflexive mechanisms of attention. In a typical peripheral cueing paradigm, participants fixate upon a central marker in the center of the computer screen. The fixation marker is symmetrically flanked by two outline boxes, one in the right and one in the left visual field. The participant's task is to detect or discriminate a target image, which randomly appears in the right or left visual field without making an eye movement. Prior to target presentation a non-predictive abrupt luminance change or new perceptual object (i.e. cue) briefly appears around the right or left peripheral box. The results from researchers using this paradigm have consistently shown that the peripheral cue stimulus reflexively

captures attention and facilitates the perception of and motor response to subsequent target stimuli (Carrasco et al., 2004; Yeshurn, 2005; Yantis and Hillstrom, 1994) This was evidenced by faster reaction times and better accuracy to the target stimulus when it was spatially preceded by the cue (cued trial) compared to targets appearing in the other box location (uncued trial). Not only is reaction time and accuracy enhanced at cued locations but so is contrast sensitivity and spatial resolution at the cued location (Carrasco, et al., 2000, 2004). That is, reflexive attention enhances our ability to detect subtle changes in luminance and discern fine details at the cued compared to uncued loactions. This finding is interpreted as reflexive attention enhancing the sensory gain at the cued location, thus making the target image appear more salient (Carrrasco, 2004; Eimer, 1993; Mangun and Hillyard, 1995).

The cuing benefits found using a peripheral cue-target paradigm are typically found only when the interval between the cue and target is short. It is believed that the cue automatically engages attention to its location in preparation to respond to subsequent stimulation. If nothing happens within a short amount of time, attention disengages from the cued locus and moves to a new location (Posner, 1980). Thus, the perceptual and behavioral facilitation effects from abrupt onsets are short-lived. As the time between the cue and target increases there is a greater chance of target inhibition at the cued location such that RTs are increased on cued relative to uncued trials. (Posner & Cohen, 1984). This inhibitory phenomenon is referred to as inhibition of return, or IOR (Posner & Cohen, 1984; see Klein, 2000 and Lupianez et al., 2006 for a review). IOR is a mechanism that inhibits attention and eye movements from returning to a previously attended/fixated location (Rafal et al., 1989; Itti 2000). This enables one to quickly search novel locations for items of importance at the expense of previously attended locations that did not contain relevant information (Klein and

Macinnes, 1999). The effects of IOR can begin as early as 100ms and can last over 1000ms (Klein 2000). The onset of inhibition is highly correlated with task difficulty such that IOR onset increases as task difficulty increases (Klein, 2000). For example, tasks requiring simple target detection reveal IOR effects sooner than a similar task requiring a difficult discrimination task (Lupianez et al., 1996). IOR also produces different effects based on spatial proximity of the cue and target. The extent of inhibition increases as the stimulus of interest gets spatially closer to the initial locus of capture (Pratt, 2001).

IOR may represent higher order processing mechanisms used to process target information. It has been shown that simple target detection tasks are more likely to show IOR attention effects when compared to discrimination tasks. A dominant theory behind the function of IOR posits that attention is inhibited from returning to a recently attended location. Humans have developed attentional mechanisms to facilitate information processing at recently attended locations in visual space; however, if no information is available at an attended location, our visual system deems other locations more important and inhibits the initial location engaged by attention. Most distractor cues used in exogenous cueing paradigms consist of a simple luminance change. Most targets requiring a detection response are also simple changes in luminance. When a basic detection task is employed, the prior cue stimulus consisting of simple luminance change likely activates response related mechanisms. On the other hand, when an exogenous cueing paradigm uses a target discrimination task, simple luminance transients are not likely to activate the same response mechanisms to the same degree.

Electrophysiological Evidence of Attentional Capture

Many of the reflexive attention effects found at the behavioral level are also seen at the neural level. Multiple stages of information processing are executed between target onset and target response. This limits the interpretation of the overall processing mechanisms involved in attention as revealed through dependent measures of reaction time. Noninvasive neuroimaging techniques enable researchers to get a clearer understanding of the temporal and spatial aspects of the attentional mechanisms involved in cognition by measuring the neural activity before, during and after target onset. Such techniques include event-related potentials (ERPs), time-locked averaged epochs of the scalp-recorded electroencephalogram (EEG), and functional magnetic resonance imaging (fMRI). Event-related brain potentials provide high temporal resolution of the neural activity as participants perform cognitive tasks. ERPs provide a direct measure of neural activity, and by analyzing the location, latency, and magnitude of the ERP waveforms one can more precisely determine the time course of mental operations.

The effects of reflexive attention have been investigated using ERP methods. Specifically, Hopfinger and Mangun (1998) recorded ERPs while participants performed a peripheral cueing task requiring two forced-choice discrimination task. Targets were equiprobable in the upper right or left visual field and were preceded by a non-predictive exogenous cue. The results indicated that attention was automatically captured by the cue and enhanced subsequent neural processing to targets presented shortly (<300ms) after attention was captured. This was revealed by significantly larger peak amplitudes of the visual P1 ERP component to targets on cued compared to uncued trials over occipital electrodes sites contralateral to the target visual field. The P1 is the first positive defelection in the ERP waveform that peaks in amplitude around 100ms after stimulus onset and is generated in

extrastriate visual cortex (Heinze et al. 1994; Mangun and Hillyard, 1991; Mangun, et al., 1997; VanVoorhis and Hillyard, 1977). The enhancement of the P1 by reflexive attention has since been replicated using different types of exogenous cues containing a luminance change (Fu, 2001; Hopfinger and Mangun, 2001; Fu, 2005; Hopfinger & Ries, 2005).

Abrupt onset cues also affect later stages of processing as indexed by the ipsilateral invalid negativity (IIN). The IIN is a more negative going component found to uncued with respect to cued target stimuli over ipsilateral scalp sites in the temporal-parietal region. This component is believed to reflect an automatic disengage/reorient mechanism of attention (Hopfinger & Mangun, 2001; Chambers et al., 2004). On uncued trials at short cue/target intervals participants must disengage their attention from the cued location and reorient to the target presented in the opposite visual field. This process is not necessary when the cue and target appear in the same location. Based on scalp topography, and previous neuroimaging data, it is likely that this disengage function arises from activity in the parietal cortex, a key structure involved in the visual attention network (Corbetta and Shulman, 2002).

Higher levels of information processing such as those correlated to the P300 ERP are also affected by an abrupt luminance change in the periphery. The P300 is believed to represent aspects of information processing such as context updating and is generally larger to unexpected or infrequent stimuli (Donchin, 1981). The P300, which shows a maximum voltage distribution over central/parietal electrodes, is significantly larger to cued relative to uncued targets in peripheral cueing paradigms at short ISIs (Hopfinger and Mangun, 1998; 2001; Hopfinger and Ries, 2005). The P300 amplitude is positively correlated to stimulus relevance and the amount of attentional resources employed in a given task (Ruchkin, Johnson, Canoune, Ritter, & Hammer, 1990; Wickens, Kramer, Vanasse and Donchin,

1983). Abrupt onsets consisting of a change in mean background luminance enhance both the P1 and the P300 to subsequent targets at short cue to target latencies suggesting that reflexive attention influences both early and late stages of information processing. This finding also indicates that recognized and attended stimuli produce a larger P300 relative to those that are unrecognized and unattended (Griffin, Miniussi, & Nobre, 2002; Rugg and Coles, 1995).

ERPs time-locked to targets at short cue to target intervals are different from those found at long cue to target intervals where IOR typically occurs. There has been some debate in the behavioral literature concerning the processing stages affected by IOR. It may be the case that IOR effects are due to degradation in early sensory attention processing or IOR may directly influence response-related processes (Klein & Taylor, 1994; Posner, 1985; Taylor & Klein, 1998). For instance, recent electrophysiological data suggest that IOR arises primarily at early attentional stages of processing. This was evidenced by larger P1 amplitudes to uncued compared to cued targets when a long ISI was used (Hopfinger & Mangun, 1998, McDonald, Ward and Kiehl, 1999; Prime & Ward, 2004). By time-locking to both target stimuli and motor responses (button presses), Prime and Ward (2004) showed that IOR is associated with a delay in premotor responses. This was evidenced by no differences in the latency of the response-locked motor response; however, the P1 and N1 ERP components had significantly reduced amplitudes on cued compared to uncued trials at the long cue to target interval.

Voltage differences between cued and uncued targets seen in the IIN and P300 components at short ISI's disappear when a long ISI is employed. These components do not display cued-uncued differences at long cue to target intervals presumably because attention has disengaged from the cued location by the time the subsequent target appears. If attention

remained engaged at cued locations at long ISIs, then subsequent uncued targets should show differences consistent with those seen at short ISIs.

Attentional Control Settings (ACS)

The above experiments suggest that an abrupt luminance transient in the periphery automatically attracts attention. However, recent RT experiments have questioned the automaticity of attentional capture to abruptly appearing stimuli at short cue to target intervals. Folk, et al., (1992) showed that an abrupt onset cue stimulus consisting of a luminance change only captured attention and speeded RTs on cued relative to uncued trials when subjects responded to targets containing similar properties (an abrupt onset target with a luminance change). However, the ***identical*** cue ***failed*** to produce RT differences between cued and uncued trials when the target of interest was defined by a unique colored item amongst multiple distractors of a different color. Researchers have since replicated these findings using various types of stimulus features. For example, it has been shown that a moving cue only speeds RTs when the observer is prepared to find moving targets, but not to colored targets without motion (Folk et al, 1994). Also in line with these findings, it has been shown that peripheral increment thresholds for color suffer when the observer is currently performing another color discrimination task at fixation but not when the central task is luminance discrimination (Morrone, Denti, and Spinelli, 2004). The reverse is true when luminance thresholds are measured. That is, when given two simultaneous visual perception tasks, task one performance decreases when task two also requires color processing; however, task one performance is not decreased when task two involves luminance but not color processing. These data suggest that attentional orienting is biased to stimuli relevant to

current task demands; moreover, luminance contrast and color may attract independent attentional resources.

A recent series of event-related potential (ERP) studies found evidence that attentional orienting is initially influenced by bottom-up feature processing and subsequently biased by top-down goals (Hopfinger and Ries, 2005). In these experiments participants made a discrimination response to a target briefly preceded by a single non-predictive luminance transient, or a non-predictive multi-element color singleton display. Half of the trials contained a cue and target defined by the same feature, such as luminance contrast or color, while the other half of trials contained incongruent cue/target combinations, such as a single high luminance contrast cue and a multi-element color target display. According to previous behavioral data (e.g. Folk et al., 1992; 1994), attending to a stimulus is contingent upon the top-down goal state of the observer. That is, only cues that match a target defining feature will attract focal attention because participants have top-down knowledge of what target features to look for. We obtained RT data that supported the contingent orienting hypothesis. However, in contrast to this view, ERPs time-locked to target presentation demonstrated that the unique luminance transient cue significantly biased early visual processing as indexed by a larger visually evoked P1 component to cued relative to uncued trials regardless of whether the features of the cue and target matched (Hopfinger & Ries, 2005). While the P1 amplitude was larger on cued trials regardless of the congruency between the cue and target, the latency of the P1 was influenced by cue/target similarity. The latency of the P1 (difference wave was expanded) was significantly longer when the cue and target were congruent (i.e. onset cue/onset target) suggesting attention remained engaged longer or facilitated subsequent target processing longer on congruent with respect to

incongruent trials due to top-down behavioral goals. Equiluminant color cues did not bias subsequent target P1 amplitude, but the same top-down effects on the IIN and RTs were observed. These data support the view that visual attention is initially reflexively biased by the abrupt appearance of a salient feature and is subsequently modulated by top-down influences.

Taken together the above experiments reveal that an abrupt change in the periphery can automatically capture attention. This is especially true when the stimulus event consists of a luminance change and is a new object, and/or is relevant to the current task at hand. Reflexive attention enhances early neural activity in extrastriate visual cortex and also influences neural activity in other cortical areas involved with disengageing/shifting attention and other attention related areas involved in target identification and discrimination. Do new luminant objects engage the reflexive attention system the same as new colored objects without luminance information? The physical characteristics of the capturing event may differentially bias early visual processing.

Magnocellular & Parvocellular Streams

Currently there is disagreement in the literature regarding the necessary and sufficient features needed to engage the reflexive orienting system. This disagreement may be resolved by considering the structure and function of the underlying visual pathways activated by stimulus features already known to trigger reflexive attentional shifts. Understanding how visual stimulation is processed prior to a shift of attention may reveal if reflexive shifts of attention are triggered in a similar fashion by all capturing events or if it is engaged differentially based on the fundamental properties of the capturing stimulus. If reflexive

attention is engaged differently based on stimulus properties, then it is reasonable to assume that the properties activate different structures/functions in the visual system.

Before we fully perceive and interpret an object or event a number of neural computations must be completed. What we see from moment to moment is the result of a complex process that combines attributes of the visual world such as spatial locations, color, movement, and brightness into a unified percept. Prior to these attributes being combined in the visual cortex, they are first processed semi-independently through multiple stages in the visual system. Specific features in the visual scene, such as color and brightness, first stimulate cones and rods respectively in the back of the retina. The stimulation is directly influenced by the wavelength frequency, luminance contrast, and location of the stimulus. Cones, which are outnumbered by rods 20:1 reside primarily in the fovea, are color sensitive, and have fine spatial resolution. They help us see color under the proper illumination and allow us to discern fine details. The three main cone photoreceptors have unique spectral sensitivities that respond to wavelengths peaking at 440 nm, 530 nm, and 560 nm. These are labled b (blue) or S (short-wavelength), g (green) or M (medium-wavelength), and r (red) or L (long-wavelength) respectively (Smith and Pokorny 1975). Rods on the other hand are located throughout the retina, are not as color sensitive as the cones, and are most sensitive to luminance information. They enable us to see at night, but only in monochrome. The rod and cone photoreceptors serve as the beginning of an internal neural signal generated by external visual stimulation.

Visual information stimulating the rods and cones is relayed to the bipolar cells and communicated on to the retinal ganglion cells. Exiting the retina via the optic nerve this information continues in parallel to the primary visual cortex via the LGN through three

primary pathways. These pathways are referred to as magnocellular (M), parvocellular (P), and koniocellular (K). The M, P, and K pathways constitute ~10%, ~80%, and ~10% of LGN neuron population respectively (Kaplan, 2004). The flow of information from the retina to LGN to V1 has been labeled the retino-geniculate-cortical pathway and constitutes 90% of the optic tract fibers (Kaplan, 2004). The other 10% are directed from the retina to the superior colliculus (SC), or the retino-collicular pathway. Most research concerning these three pathways have focused on the M and P pathways; only recently has the structure and function of the K pathway been studied.

Current evidence suggests the K pathway responds to triton (blue-yellow) stimuli and may play a role in motion processing. Moving triton stimui, which activate the S cones (blue sensitive) and K pathway, have been shown to produce earlier unique electrical fields when compared to electrical fields generated by moving achromatic stimuli (Morand et al., 2000). This finding is consistent with monkey data showing some K neurons bypass V1 altogether and directly innervate area MT, the primary motion processing region in the macaque (Sincich, Park, Wohlgemugh, and Horton, 2004). Due to the paucity of research on the K stream in humans, the main focus of this proposal is on the M and P pathways, which have been studied more extensively. While our stimuli designs are not guaranteed to completely isolate the influences of the K stream, our key manipulations shy away from K stream activation by using either achromatic motion at low spatial frequencies and low luminance contrast for targeting the M stream or chromatic (red or green) high spatial frequencies for targeting the P stream.

Visual information activating the rods and cones is transmitted to bi-polar and ganglion cells in the retina. This information is then propagated to the LGN, which consists

of six distinct cell layers (Kaplan and Shapley, 1986; Livingstone and Hubel, 1988; Kaplan et al., 1990). The two dorsal layers make up the M stream while the ventral four layers constitute the P stream. After synapsing in the LGN visual information continues to the primary visual cortex (V1) also consisting of six functionally distinct layers. Cortical cells displaying characteristics of high contrast gain such as M cells are found in layer 4Cα and color-opponent neurons, which are the targets of LGN afferents from P cells are found in 4Cβ in V1 (Hawken, Parker and Lund., 1988).

Both the M and P streams have unique characteristics in that they have different response properties and convey different types of information to the cortex (see Table 1 for a summary of M and P characteristics). The M stream has a fast conduction speed, favors stimuli that move and/or contain subtle increments in luminance contrast. It is relatively color blind and is sensitive to low spatial frequencies. The P stream on the other hand contains much smaller cell bodies and has a slower conduction speed when compared to the M stream. High spatial frequency, color (preferably isoluminant with surround), and mid to high luminance contrast are the primary features that stimulate the P stream (Kulikowski et al., 2002).

While M and P streams respond differently to spectral information, another aspect that dissociates these streams is contrast gain. Responses in M neurons increase more rapidly than P neurons as contrast increases (Kaplan and Shapley, 1986). That is they are sensitive to subtle changes in luminance contrast. While magnocellular neurons are sensitive to luminance contrast, their responses begin to saturate around 30% contrast (Shapely, 2004). Parvocellular neurons, however, respond very little to low contrast stimuli, but they do become active at high luminance contrasts. See Table 1 for a list of common M and P

properties. Luminance contrast is referred to as the variation in the light a stimulus contains, normalized by the average amount of light (Shapley, 1990). For example a lightning bolt has a higher luminance contrast at night than during the day. Luminance contrast is typically defined as C = (Lmax -Lmin)/(Lmax + Lmin), where C = contrast, L= luminance in candels per meter squared and is commonly referred to as Michelson contrast. (Michelson, 1927).

While there is some cross-talk between the M and P streams prior to V1, much of the processing remains segregated. This even holds true to a certain degree beyond primary visual cortex. After processing in V1, information is partially segregated and diverted either dorsally or ventrally depending on innervating responses. The dorsal or 'where' pathway responds selectively to spatial locations of stimuli and direction or speed of motion (Desimone and Ungerleider, 1989). The dorsal stream projects to areas MT, STS, and posterior parietal cortex. The ventral or 'what' pathway responds primarily to features necessary to identify an object. This includes features such as shape and color (Desimione and Ungerleider, 1989). The 'what' pathway comprises more ventral areas such as the inferior/temporal lobe (Ungerleider and Mishken, 1982).While these two streams are not completely independent, magnocellular and parvocellular activity are predominately activated by movement or isoluminant color in the dorsal and ventral streams respectively (Ferrera, Nealy, Maunsell, 1994). Thus, visual brain regions encoding early visual input are driven primarily by bottom-up mechanisms such that inputs at the retina are transmitted through successive stages of processing with little cross-talk up through the ventral and dorsal processing streams (Ungerleider and Pasternak, 2004).

Response properties of the retino-geniculo-cortical pathway indicate feature driven activity simply based on spatial frequency is capable of primarily activating either the M or P

visual stream . Breitmeyer (1975) demonstrated that RTs to high spatial frequency stimuli are prolonged compared to those to low spatial frequency even when luminance contrast is kept constant. This finding is consistent with the response properties of the P and M streams respectively in that parvocellular cells have a more sluggish response compared to magnocellular cells.

It has also been established that stimuli activating the M stream are identified more accurately than stimuli activating the P stream. This evidence is based on the finding that solitary isoluminnat letters presented in the periphery were identified and responded to equally well when compared to a letter with a low luminance contrast. However, when the P target letter was flanked by two isoluminant P letter distractors, responses times and errors increased compared to when low luminance contrast target stimuli were used (Omtzigt and Hendricks, 2002). From this finding the researchers concluded that M stream activation triggered by the luminance contrast target attracted attention, for when the location of the flanked letters were known ahead of time and voluntarily attended to, the color/luminance contrast differences disappeared (Omtigt and Hendricks, 2004). In other words, when target location was unknown prior to its appearance, magnocellular activation aided in target identification for both single and flanked targets; however, target identification suffered to flanked targets that were isoluminant but not to isoluminant targets presented in isolation. The discrepancy between single and flanked targets disappeared when target location was known ahead of time. This is because voluntary attention helped boost or bias the target signal, thus decreasing the effect of isoluminant flanked letters serving as distractors.

Given M and P streams have different early electrophysiological responses based on luminance contrast, later processing stages based on RTs also reveal underlying M and P

activation to stimuli with varying degrees of contrast. Recently Murray and Plainis (2003) obtained RTs to stimuli varying in luminance contrast, duration, or eccentricity. They found a clear dissociation in RT between high and low contrast indicative of response characteristics corresponding to P and M pathways respectively. In conditions with 10-15 degree eccentricity a single linear function accounted for the data; however, a clear bi-linear RT contrast function provided the best fit for data when stimuli were less than 10 degrees in the periphery and/or relatively low in spatial frequency, <5.5 c/deg. This showed that the first linear function fit the data with the least residual variance for stimulus contrasts up to 10%. The second function provided a best fit to data above 10% contrast. The fitted lines above and below the 10% contrast point were interpreted as activity reflected by P and M streams respectively. M stimuli elicited a faster response than stimuli primarily activating the P stream. This implies that overt reaction times occurring at late stages of cognitive processing are directly related to early visual processing characteristics. Saccade latencies are also influenced by spatial frequency and luminance contrast similar to RTs. Saccade latencies are known to decrease as a function of contrast and increase as a function of spatial frequency (Ludwig, Gilchrest, and McSorley, 2004). Response differences observed in behavioral data between M and P activation are also found in electrophysiological brain activity.

M and P Electrophysiology

Visual evoked potentials (VEP) in humans reveal characteristics of both M and P stream activation. The onset of isoluminant chromatic gratings produce spatially distinct and more temporally sustained responses when compared to achromatic stimuli, which corresponds with response characteristics of these systems observed in primates (Kulikowski et al., 2002). Since the chromatic grating contained only color information and little if any

luminance information, it was assumed the waveforms mainly reflected the activity of the P stream. A recent study by Ellemberg et al., (2001) found that early visual ERP components such as the P1 and N1 also showed selectivity to M and P activation. The P1 had a typical magnocellular response in that it appeared at low contrasts and increased as contrast increased but only up to medium contrasts where it saturated. The N1 component however, displayed characteristics of the parvocellular stream. As spatial frequency increased, so did the magnitude of the N1**.** Varying the spatial frequency of a stimulus results in different morphologies of VEPs suggesting they activate different processing mechanisms in the brain. Low spatial frequency gratings tend to produce a larger and faster P1 component compared to gratings with a high spatial frequency (Skandies, 1984; Proverbio, 1993). Prior to the P1, an early negative component (N70) has been reported to be evoked primarily by high spatial frequency gratings (Reed et al., 1984; Proverbio, 1993). A recent VEP study found similar results to square-wave gratings presented at the fovea. VEP studies typically present stimuli at fixation consisting of flashing lights, gratings or checkerboards that evoke occipital responses at the onset of different patterns and or contrasts. Analysis of the VEP activity showed different distributions of activity to stimuli based on their spatial frequencies. Low frequency stimuli elicited a bilateral occipital positive potential; however, high frequency gratings evoked a prominent negative potential over midline electrodes at the same time range, 60-120ms (Proverbio et al., 1996).

Motion, which primarily activates the M stream, also displays unique characteristics in the VEP waveform. While the P1 is rather insensitive to temporal frequency, the N200 is parametrically modulated by the speed of motion. As the motion speed increases, so does the amplitude of the N200. A low spatial frequency moving stimulus elicited smaller P1 and N1

ERPs compared to a high spatial frequency, stationary color grating. This result corresponds to the relative processing speed of the M with respect to the P stream at low contrast. Moving stimuli, however, evoked faster P1 and N1 latencies compared to the color stimuli presented for the same duration (Mitchell and Neville, 2004). This finding corresponds to the speeded conduction of magnocellular compared to parvocellular neurons in the visual system.

Evoked potentials also reveal different responses to chromatic and achromatic stimuli even when they are equated by spatial frequency or luminance contrast. Using chromatic and achromatic grating onsets, Kulikowski and colleagues (1989) demonstrated that red/green stimulation evoked a negative response while the achromatic stimulation at the same spatial frequency evoked an opposite positive component at the same latency. This study went on to show that VEPs evoked by red/black or green/black were very similar and indicated activity of an achromatic channel; however, isoluminant stimulation produced a color-dependent signal (Kulikowski et al., 1989).

The color red appears to receive processing priority over other colors. Red stimuli produced 140-350% increases in signal amplitude in the P terminating layers in V1 when compared to achromatic stimulation. Interestingly, green stimuli did not significantly increase the signal in these same layers (Givre, Arezzo, and Schroeder, 1995). VEPs evoked by chromatic stimulation contain an additional red sensitive component when compared with VEPs elicited by achromatic stimulation at the same contrast (Klistorner et al., 1998). VEPs evoked by green-gray stimuli and achromatic stimuli produced similar waveforms when compared at different luminance contrast values. However, red-gray stimuli elicited a response that differed in waveform, amplitude, and peak latency from that seen with achromatic stimuli at the same contrast. These findings are not surprising given there are

more red sensitive cones in the retina and little if any convergence occurs from retinal ganglion output to V1.

Evidence of Attentional Capture from M and P Streams

The M stream has been implicated as a key pathway in triggering attentional capture. "The magnocellular visual pathway is known to be quite sensitive to high temporal frequency, and one of its functions might be to signal the location to which attention should be directed" (Egeth and Yantis 1997, p. 274). This is a reasonable assumption given that luminance contrast, which stimulates the M system, produces larger deflections in early visual ERP amplitudes and shorter RTs to stimuli increasing in luminance contrast (Kammer, 1999). The magnocellular system is directed dorsally from V1 to the parietal cortex, which is a primary brain region in the neural network underlying shifts of visual attention. Therefore, it is reasonable to assume that as the contrast of a stimulus increases so does its probability of activating the parietal cortex and triggering a shift of attention. Many experiments have provided evidence in support of the M stream domination in attentional capture.

Using a line motion illusion paradigm, Steinman et al., (1997) found evidence that attention is primarily driven by the M stream. In this study, peripheral luminance cues produced larger attention effects compared to isoluminant color cues. Furthermore, when luminance contrast cues were presented shortly after the presentation of an isoluminant color cue, the luminance cue still dominated the competition for attentional resources. This is likely due to the fast conduction speed of the M stream catching up to and overriding the P stream activation; therefore, sooner activating the reflexive attention network (Steinmann et al., 1997).

M stream dominance in attentional orienting is not only found in peripheral cueing paradigms. In a visual search task subjects performed a conjunction search for the presence or absence of targets that were isoluminant with the background or contained small luminance contrast values (2% or 5%). As expected, RT increased as a function of set size due to more competition for attentional resources as the number of distractors increased. Interestingly, luminance contrast targets were identified significantly faster when compared to isoluminant targets at each display size. Overall, the results demonstrate that serial searches requiring visual attention become slower when stimuli are isoluminant with the surround compared to when they contain a contrast in luminance (Cheng, Eysel, & Vidyasagar, 2004).

Data from brain damaged patients also shows an advantage of the M stream in attention and performance. When compared to healthy controls, neglect patients show poor accuracy to luminance targets presented in the contralesional (left) visual field (Pitzalis, Di Russo and Spinelli, 2005). However, accuracy was not different between the groups when chromatic stimuli were used. The authors claim neglect patients have a selective deficit in the magnocellular pathway since the M stream has many projections to the parietal cortex. However, it may not be necessarily a deficit to the M stream per se but just that the M stream information is not successfully processed in regions that require a shift of attention to perform adequately.

While the above research suggests that luminance contrast stimuli produce both capture and inhibition, it is still unclear what role color, specifically parvocellular activation by isoluminant color, plays in capturing attention. Only recently have researchers begun to focus on the parvocellular stream in reflexive capture. Evidence supports the idea that

isoluminant color cues engage reflexive attention mechanisms and produce similar costs/benefits in RTs as those found in studies where cues primarily consist of a luminance contrast or M stream activation. To prevent luminance from contributing to attentional capture, Snowden (2002) presented random luminance noise in the background during a non-predictive peripheral cue/target paradigm using isoluminant color cues. This was done to keep luminance processing constantly active and presumably unable to contribute to attentional capturing processes. This study demonstrated that a non-predictive abruptly appearing color cue automatically captured attention as determined by faster RTs to cued relative to uncued targets. However, the cue in this case consisted of a color change as well as a new object. The color change could also be perceived as a unique object, so it is not clear if color alone captured attention or whether the colored object captured attention.

This led researchers to use the same paradigm with the same stimuli but include an old object condition where only a color change to an omnipresent object occurred (Cole et al., 2005). When this old object manipulation was added, the researchers found that only the new objects captured attention and not simply a unique color change. It was concluded that a unique color change alone cannot capture attention but is instead captured by the presence of a new object.

Recently, however, this conclusion was challenged. The same experiment done by Cole et al. was performed only the duration of the cue was manipulated (Lu, 2006). In Cole et al's study the cue was only 50ms in duration. Lu reasoned that since the parvocellular system has sluggish response the lack of capture may not have completely activated the P stream; therefore, Lu used the same paradigm as Cole et al but used five different cue durations. Lu replicated earlier findings with the 50ms duration condition, which did not

show evidence of capture. Attention was captured by a color change to an old object when the cue duration was 75, 100, 125, and 150ms. This finding lends support to the claim that in order for reflexive attention to be engaged by the P system, the stimulus triggering attentional engagement must be present long enough to completely stimulate the P stream. It may be the case that in previous studies using P targeting stimuli to activate reflexive attention mechanisms did not provide adequate stimulus durations to fully activate the P stream.

Rationale for Proposed Studies

Based on the paucity of data and shortcomings in prior studies it is still not clear how M and P stream activity uniquely contribute to reflexive attention. It is known that voluntary attention mechanisms influence non-spatial target properties, such as color, spatial frequency, and direction of motion, in brain regions that primarily process these attributes (Kenemans, et al., 1993; Anllo-Vento and Hillyard, 1996). However, little research has focused on how non-spatial target properties influence the allocation of attention. It has been suggested that stimuli activating the M stream such as abrupt onsets with luminance contrast are responsible for activating the reflexive attention system (e.g. Steinman et al., 1997); however, current experiments suggest stimuli that activate the P stream, such as isoluminant color cues, may be equally important for initiating reflexive shifts of attention (Yeshurun, 2004; Lu, 2006). The studies addressing the effectiveness of isoluminant color cues on attentional capture have also simultaneously presented random luminance noise in the surround (Snowden, 2002, Cole et al., 2005; Lu, 2006). This was done to control for potential M stream influences since it was presumably always active. Therefore, it is still unknown if P stream activation alone can trigger a reflexive shift of attention in the absence of M stream activation.

The neural mechanisms of M and P stream activation in relation to shifts of attention are also unknown. Electrophysiological studies of reflexive attention have not directly manipulated M or P stream activation to assess the underlying pathways responsible for reflexive shifts of attention; in fact most electrophysiological experiments of reflexive attention have used high luminance contrast and mid to high spatial frequencies, which would activate both the M and P systems. To assess the unique contributions each system has on reflexive visual orienting, it is important that stimuli activate one or the other system but not both simultaneously.

Another limitation in previous research addressing M and P function is that many experiments only recorded brain activity from a small number of electrodes, mostly one placed at Oz, which is the in the center of the head over the occipital lobe. Therefore, it is difficult to interpret the spatio-temporal properties of M and P function in the brain. Employing higher electrode densities would provide more accurate spatio-temporal processing characteristics of the M and P pathways. This is accomplished by measuring electrical activity from electrodes in close spatial proximity. Subtle differences between the timing and magnitude of neural signals cannot be detected as easily with a small number of electrodes (<64) because there is greater interpolation required as the distance between electrodes increases. By increasing the number of electrodes more accurate estimates can be obtained to identify the neural structures giving rise to the scalp recorded activity.

To date, most studies investigating IOR have employed cue stimuli with luminance contrast; therefore, it is also undetermined if M and P activation results in similar inhibition of return (IOR) effects. It has been demonstrated that ‘S cone’ stimuli, which do not activate the M stream, can still produce IOR but only in manual RT response and not in saccade

responses (Sumner, 2006). However, luminance stimuli targeting the M stream produced IOR when using both manual and saccade responses. This suggests that stimuli that bypass the retino-collicular pathway are still able to trigger IOR.

Finally, it is not known if top-down contingencies (i.e. congruency between cue and target properties) for M and P stimuli differentially influence the amplitude and/or latency of the visual occipital P1 component. Recent behavioral evidence suggests that isoluminant color cues capture attention only when subjects are looking for an isoluminant target, and not targets with luminance (Lambert et al., 2003). It is important to know if processing mechanisms engaged prior to manual responses also show this finding. Specifically, is the P1 and P300 enhanced on cued relative to uncued trials at short ISIs, and do uncued targets display an increased negativity compared to cued targets over ipsilateral occipital/parietal electrodes?

The present experiments directly address the questions and limitations above by: 1) designing cue stimuli that primarily activate either the M or P pathway, 2) measuring neural activity with high electrode densities (96 electrodes) to M and P cues and targets, which provides a precise temporal measure of cognitive operations 3) varying the interval between the cue and target in order to measure potential IOR effects, and 4) inducing subjects to adopt particular top-down task goals by varying the type of target they respond to. By manipulating and isolating these variables I was able to independently assess the contributions of the M and P visual systems on reflexive orienting.

This paper first reports data from two pilot studies. The purpose of the first two pilot experiments was to design cue stimuli for subsequent peripheral cueing experiments that primarily activate either the M or P processing stream. Based on prior electrophysiolgical and

psychophysical data, we constructed stimuli with predominately M or P features. The stimuli most consistent with M and P activation were used as cues and provided the feature parameters used for M and P targets in two subsequent peripheral cueing experiments.

Pilot Studies 1 & 2

Only slight differences in stimuli were used between Pilot studies 1 and 2; therefore, the methods for the two pilot studies are presented together.

Method

Participants

Five healthy college-aged volunteers participated in each pilot study (Pilot 1- 3 females, average age 20.4yrs; Pilot 2 – 4 females, average age 22.1yrs.). All participants provided informed consent, were right-handed, had no known neurological problems, and had 20/20 or corrected to 20/20 vision. Each participant was reimbursed $10 for each hour of their time.

Materials and Procedure

In each pilot study participants were instructed to fixate a small star located in the center of a CRT computer monitor 65 cm ahead. Their task was to make one of two possible responses on a game pad based on the color of an infrequent target square, which was either blue or yellow and could appear randomly in the upper/lower, right/left quadrant of the computer screen. On all other trials participants were instructed to withhold response and remain fixated on the center marker. Non-target trials consisted of one of five possible stimuli presented in the upper right, upper left, or in the center of the visual field. Potential stimulus locations were designated by an outline box subtending 5.3x5.3°. A smaller outline box subtending 2.3x2.3° was placed in the middle of each larger box (Figure 1). The

placeholders were designed to appear as individual objects. The center of each peripheral placeholder was 9.7° from the center of the central fixated placeholder. On each non-target trial one of the three object placeholders underwent an abrupt change that was designed to primarily activate either the M or P processing stream. In the first pilot study, the stimuli consisted of a high frequency (8 cycles per degree) isoluminant red grating, or a low frequency/low luminance flash presented for 75ms. The above manipulations have been used in previous electrophysiological and single cell experiments to activate either the M or P stream (Ellemberg et al., 2001; Klistorner et al., 1998; Kulikowski et al., 2002); however, unlike the studies presented here, prior studies presented stimuli mainly at fixation and electrical brain activity was only measured from a small number of electrodes.

The second pilot experiment was similar to the first with the addition of four new stimuli designed to target either the M or P stream. One of the M stimuli was a low spatial frequency low contrast gabor moving left to right at a temporal frequency of 16hz. The other M stimulus was a low spatial frequency gabor with a 75% Michelson contrast. This stimulus was designed to be paired with a high frequency (10 cycles per degree) stimulus of the same contrast. It has been shown that stimuli with low and high spatial frequency manipulations controlling for luminance contrast activate different neural mechanisms at early levels of visual processing and also result in reaction times that correlate to the processing speed of the M and P streams (Mitchell and Neville, 2004; Murray and Plainis, 2003). The other P-targeting stimulus in the second pilot study was an isoluminant green grating. This was used in addition to the red grating not only because prior studies have demonstrated these stimuli activate the P stream but also because previous literature has shown a unique response to red stimuli compared to green (Klistorner et al, 1998).

It was predicted that the color and high spatial frequency stimuli (P stimuli) would elicit different ERP waveforms over occipital scalp sites compared to achromatic stimuli consisting of low luminance contrast and low spatial frequency (M stimuli). Specifically, it was predicted that M stimuli would elicit early visual potentials faster than P stimuli, consistent with the M and P processing characteristics. It was also predicted that all foveal stimuli would produce a greater response compared to peripheral stimuli due to the number of retinal ganglion cells present near the fovea.

Pilot 1 Results

The ERP waveforms to stimuli designed to primarily activate either the M or P visual stream revealed distinct characteristics consistent with one or the other stream. The primary distinction was seen between the red, high frequency grating and the low frequency, low luminance contrast flash. As seen in Figure 2 and in line with previous electrophysiological data assessing M and P responses, the high spatial frequency red stimulus produced an early negativity that was absent in the low spatial frequency, luminance contrast stimulus. Also, the stimulus targeting the M stream elicited a foveal P1 ERP that was absent in the P stimulus waveform. While these results were true for stimuli in the central visual field, similar effects were not found to stimuli presented in the periphery. In fact, we obtained very weak responses from the peripheral stimuli. Pilot experiment 2 was designed to see if other stimuli known to target either the M or P stream would reveal similar results or if the lack of a peripheral response was specifically due to the stimuli we used. Pilot study 2 also allowed us to potentially replicate the results of Pilot 1 by using the same stimuli in addition to four others.

It was predicted that ERPs would be similar to those found in Pilot 1 to the red grating and low luminance stimulus. It was expected that the motion stimulus and low spatial frequency stimulus (M-targeting) would evoke significantly different responses when compared to the green grating and high spatial frequency stimulus (P-targeting). Specifically, it was predicted that the M targeting stimuli would elicit a P1 that was absent in the waveform produced by the P targeting stimuli. It was also predicted that similar components evoked by M and P stimuli would reveal earlier peak latencies to M stimuli compared to P stimuli. Also in line with previous research (e.g. Klistorner et al., 1998) it was believed that the red grating would produce a unique 'red' effect compared to the green grating.

Pilot 2 Results

In line with our predictions the M-targeting stimuli activated different neural generators than P-targeting stimuli based on the differences seen in the ERP waveforms. As seen in Figure 2, the responses to the red grating and low luminance stimulus were similar to those in the first pilot experiment suggesting activation of the P and M streams respectively. It is also evident that foveal ERPs to low spatial frequency stimuli produced an early positive response, while the high spatial frequency produced an early negative response at the same latency. This finding replicates previous ERP data to high and low spatial frequency stimuli presented at fixation suggesting activation of the P and M visual streams respectively (Proverbio et al., 1996). M and P stream differences are also apparent when comparing the red and green grating stimuli to the motion stimulus. At fixation, the motion stimulus produced a P1 that was absent in the waveforms elicited by the other two stimuli. Also in line with our predictions, the red grating produced a unique early response around 100ms when compared to the green grating while their responses were very similar just 50ms later. Again,

the peripheral stimuli generated a very weak response. For the intents and purposes of the proposed studies it is important to obtain a visual ERP that contains obvious P1 and N1 components like those elicited in the central visual field. It is known that chromatic and achromatic acuity decreases as the distance of the test stimulus increases from the fovea and that visual evoked responses decrease as a function of eccentricity (Anderson, Mullen and Hess, 1991; Meredith and Celesia, 1982). It is likely our stimuli were located too far in the periphery to generate a significant ERP; therefore, we have moved the two peripheral locations 3.7° toward the center. This resulted in the center of the peripheral placeholders subtending 6° from central fixation. This is within the visual angle used in previous behavioral and electrophysiological experiments employing a peripheral cueing paradigm (Bennett and Pratt, 2001; Berger, Henik, and Rafal; Hopfinger and Mangun, 1998, 2001; Hopfinger and Ries, 2005; Pratt, Hillis and Gold, 2001).

Rationale for ERP Experiments 1 & 2

Many ERP studies employing a peripheral cueing paradigm have used cues that likely activated the magnocellular system or both the magnocellular and parvocellular systems simultaneously (Fu et al., 2001; Hopfinger and Ries, 2005; Steinman et al., 1997). It is still unclear if primary activation of the parvocellular system alone can trigger a reflexive shift of attention. If it can, are the attention effects different from those activated by the magnocellular system that show neural and behavioral enhancements at short cue to target intervals and inhibition or IOR at long intervals. It is also unclear if top-down task goals, such as looking for an M or P stimulus, affects capture differently based on the preceding M or P cue distractor. Prior psychophysical and electrophysioloical data have indicated unique characteristics indicative of either the magnocellular or parvocellular system. We designed

stimuli that target one or the other system based on these data and obtained evidence in agreement with earlier research, thus indicating our stimuli were activating the correct systems (e.g. M stimuli processed faster than P stimuli). We used these stimuli as cues and targets in a peripheral cueing paradigm while measuring ERPs and behavior to get an accurate temporal measure of the cognitive mechanisms underlying attentional capture from the M and P streams. The present ERP experiments go beyond prior reflexive attention studies by directly manipulating M or P activation by the cue stimulus, the M/P cue/target contingency, and the interval between the M or P cue and the M or P target.

Experiments 1 and 2

General Method and Procedure

Experiments 1 and 2 used the same stimulus placeholders as in the pilot experiments only they were located 6° in the periphery not 9.7° and employed a standard exogenous peripheral cueing paradigm. The two stimuli that displayed neural signatures most consistent with either an M or P activating stimulus from the pilot studies were used as target stimuli in Experiments 1 and 2. The two stimuli chosen were the red grating stimulus to target the P stream and the low contrast motion stimulus to target the M stream.

Each experiment employed a similar design and contained 16 healthy, right-handed individuals. All subjects had normal or corrected to normal (20/20) color vision. Subjects were seated approximately 80cm from a computer monitor in a dimly lit room. They were required to remain fixated on a plus sign located in the center of each stimulus display presented on the computer monitor. Eye movements were observed with a closed-circuit video camera. All stimuli were presented on a medium gray background (RGB color coordinates = 127,127,127). On each trial a non-predictive abrupt onset M (dim luminance

contrast, low spatial frequency 1c/d, motion 16hz) or P (isoluminant colored grating, high spatial frequency 9c/d) cue randomly appeared in the upper left or right visual field. A P target used in Experiment 1 or an M target used in Experiment 2 randomly appeared for 75ms in the upper left or right visual field. Based on prior behavioral studies 75ms is long enough duration to engage the reflexive attention system through P stimulation. The target required a horizontal/vertical discrimination response in Experiment 1 and a right/left discrimination response in Experiment 2. Half the time the target appeared in the same location as the preceding cue (cued trials) and the other half it appeared on the opposite side of the cue (uncued trials).

A discrimination task was employed in order to limit the overt response-related activation elicited by cue stimuli. All cue stimuli consisted of a simple feature change in the periphery. Target stimuli, on the other hand, consisted of a stimulus requiring a response beyond simple feature detection. Thus, any effects of reflexive attention at early stages of visual processing are not likely to be the result of response related biasing due to the alerting effects of the cue but rather sensory or attentional biasing.

Varying the target type between experiments induced subjects to adopt a top-down strategy for either M or P target properties. All cue displays were non-predictive of the subsequent target, thereby giving the participants no incentive to attend to them. Participants were told of the cue-target contingency and instructed to ignore the cue display and simply respond as fast and as accurately as possible to the targets. Trials were separated by 1100-1500ms. Each experiment used a short and long cue to target interval or ISI. The cue/target interval was manipulated to assess potential enhancements in target responses at the short ISI

and inhibition or IOR effects at the long ISI. Each experimental condition contained approximately 100 samples to obtain a good signal to noise ratio.

As in the pilot experiments, P stimuli were isoluminant with the background in order to stimulate the P stream and help prevent activation of the M stream by luminance contrast. Isoluminance was tested for each subject prior to each experiment and measured using the minimally-distinct border method (MDB; Boynton and Kaiser, 1968). This method requires participants to adjust the luminance value of one of two juxtaposed stimuli so that the apparent border between the two stimuli is minimal. In the current studies, participants adjusted the red luminance value so that it matched the luminance of or created a minimally distinct border when compared to the gray background color stimulus.

Experiment 1 – M and P Cues, P Target

Methods

Participants

Participants consisted of 16 (5 females) healthy, right-handed adults (average age 26.2 years) and were reimbursed $10 per hour for their time.

EEG Recording

Over the course of the experiment we obtained five dependent measures that included accuracy, RT, and target P1, IIN, and P300 ERP components. EEG was recorded from 96 electrode sites, referenced to the right mastoid, amplified at a bandpass of .01-100Hz and digitized at 250 samples per second. Electrodes located beneath and lateral to the outer canthus of each eye recorded the electro-oculogram. All trials containing eye movements or blinks were rejected off-line and not included in the analysis. EEG was averaged by experimental condition to create ERP waveforms. The ERPs were low-pass filtered to

remove high-frequency noise and high-pass filtered with a single-pole causal filter to reduce low frequency drifts. Due to the close temporal proximity of the cue and target it is important to remove potential overlap of the cue activity from target activity. This was performed using the adjacent response filter or Adjar technique (Woldorff, 1993). This technique has been used previously to successfully remove the overlap target ERPs (Fu et al., 2001; Hopfinger and Mangun, 1998, 2001; Hopfinger and Ries, 2005; Hopfinger & West, 2006; Talsma, 2005).

Materials and Procedure

In Experiment 1, a P-target image randomly appeared in the middle of one of the placeholders (i.e. in the center of the small box) just prior to target presentation. The interval between the cue and target was either short (12-212ms) to assess the potential neural enhancements in target processing traditionally seen at this short interval or long (712-912ms) to assess IOR effects. The inter-trial interval was 1200-1500ms. Targets in the first experiment consisted of a P-pathway target (isoluminant red grating, 9c/d) oriented horizontally or vertically. Participants were instructed to make a horizontal/vertical discrimination response by pressing one button with the right index finger if it was horizontal and their right middle finger if it was vertical (see **Figure 3** for an example of the trial sequence). Cue presentation was completely random and in no way indicative of where the subsequent target occurred. Targets appeared in each location with the same probability. This presumably left participants with little incentive to attend to the cue. Thus, the main manipulations in Experiment 1 included: the validity of the cue, congruency between the cue and target and inter-stimulus interval. The P target was used here to induce subjects to adopt a top-down setting for P stimuli.

A fraction (9%) of trials contained 'catch' trials or trials that contained a cue but not a target. This was implemented to get a measure of cue activity with and without subsequent targets and to prevent subjects from anticipating the response of an upcoming target.

Data Analysis

Reaction times and ERPs were computed from artifact-free (no eye-movements, no eye blinks) and correct trials. Trials containing target responses less than 200ms and greater than 1000ms were discarded prior to analysis. Repeated-measure ANOVA's were employed to analyze the RT, accuracy, and ERP data. The primary dependent variables were mean RT, percent correct, and P1, IIN, and P300 ERPs. The main factors in the analysis included cue type (M or P), spatial relationship between cue/target (cued or uncued), target visual field (left or right), and for the ERP data, electrode location. Two electrodes were chosen in each condition that corresponded to electrode locations used in previous reflexive attention studies (e.g. Hopfinger and Mangun, 1998; 2001; Hopfinger and Ries, 2005). Medial occipital electrodes were near 01/02 in the 10/20 electrode location system (Jasper, 1958). Lateral occipital electrodes corresponded to T5/T6 and midline electrodes corresponded to F/Cz, Cz and Pz.

Experiment 1 Predictions

Behavior

We expected to find normal reflexive cueing effects at short ISIs where cued targets are responded to significantly faster and more accurately than uncued targets. Based on previous behavioral data it was also believed that cueing effects would be larger when the cue and target properties were congruent (Ansorage and Heumann, 2003), i.e. P cue/ P target in the present experiment. Predictions for the behavioral results at the short ISI were different

from those at the long ISI. It was predicted that cued trials would have significantly slower RTs when compared to uncued trials due to an inhibition of returning attention to the cued location. Overall we hypothesized that target accuracy would be better at the short ISI compared to the long ISI due to the perceptual enhancement of attended information.

P1 Short ISI

Based on prior literature (e.g. Hopfinger & Ries, 2005) it was believed that if both M and P cue stimuli captured attention in a similar fashion then the P1 would be enhanced on cued relative to uncued targets over contralateral electrode sites regardless of the relationship between the cue and target. However, if attentional capture is contingent upon target response properties then P cues should only capture attention when looking for P targets thereby producing an enhanced P1 only for P targets preceded by P cues but not M cues. Considering the temporal processing characteristics of the M and P pathways, I also believed P targets overall would be processed more slowly than M targets. Also, target enhancements on cued trials were predicted to occur later when compared to M targets.

P1 Long ISI

We also hypothesized that the P1 would be reduced or similar to cued relative to uncued targets over contralateral electrode sites regardless of cue/target contingency if both M and P cue stimuli produce similar reflexive shifts of attention. However, if P cues only capture attention when looking for P targets then it was expected that the difference in P1 amplitude between cued and uncued targets would be smaller for M targets compared to P targets. This would indicate that top-down control settings can influence early levels of visual processing through activation of the P stream.

IIN Short ISI

For the IIN component we hypothesized that similar IIN effects would be observed in congruent and incongruent conditions if a reflexive shift of attention is initiated to both M and P cue stimuli independent of top-down goals (in this experiment discriminating a P-activating target). If this pattern is found then it suggests that both M and P stream activation can trigger a reflexive shift of attention at relatively early stages of visual processing. However, if involuntary attentional shifts are moderated by top-down cue/target contingencies, then we expected the IIN to differ between P cue/P target and M cue/P target trials. This would indicate that the IIN is affected by the contingency between the cue and target. It must be noted the exact function of the IIN is not known. For example, depending on whether the function reflected in this component is disengaging attention or reorienting attention, it may be that the M and P cues may trigger a reflexive shift of attention but disengaging from a P cue may take longer due to the slower processing compared to the M stream.

IIN Long ISI

For the long ISI, it was believed that the IIN would be absent to targets preceded by either an M or P cue. The IIN is believed to reflect an automatic disengagement or reorienting of attention from a cue to the sudden appearance of a target in a different location. However, when the interval is increased between the cue and target, attention is able to disengage and reorient elsewhere without being reflexively drawn to a different stimulus. Therefore, if capture is similar to M and P cues regardless of top-down settings then the IIN was believed to be absent in each case because attention will have disengaged by the time the target appears. However, if IOR is moderated by top-down cue/target

contingencies, then the IIN may appear on congruent trials since attention may stay engaged at the cued position longer when the cue matches top-down expectations.

P300 Short ISI

It was expected that if M and P cues trigger a reflexive shift of attention independent of top-down goals, then similar enhancements in the P300 would be seen in congruent and incongruent conditions to cued relative to uncued target trials. This would indicate that late stages of visual processing are directly affected by reflexive attention and minimally influenced by top-down task goals. If the P300 is sensitive to recognition and context updating and is independent of prior sensory stimulation then it was believed that the cued/uncued difference would be greater on P cue/P target trials than on M cue/P target trials since P targets in this experiment are only congruent with the P cues.

P300 Long ISI

Similar P300 differences between cued and uncued targets were predicted for both congruent and incongruent trials given both M and P cues trigger similar reflexive shifts of attention independent of top-down goals. However, if the P300 is sensitive to cue/target congruency then we believed the cued/uncued difference would be greater on congruent compared to incongruent trials.

Experiment 1 Results

The primary focus of the present research is on the effectiveness of stimuli targeting the M or P system in triggering a reflexive shift of attention that results in sensory/motor enhancement and/or inhibition. Furthermore, the effectiveness of stimuli targeting the M or P system in capturing attention was assessed by varying the congruency of the cue and target. In order to assess the effectiveness of attentional enhancement/inhibition, trials in which the

cue and target occurred in the same location (cued trials) are compared with trials where they appeared opposite from each other (uncued trials). Thus, the main focus of the results section is on the main effect of cue validity and its potential interactions with short and long cue/target intervals and with congruency between cue and target. The validity of the cue never significantly interacted with visual field, so right and left visual field locations were collapsed to simplify the analysis. While visual field was collapsed, data were still able to be analyzed over contralateral and ipsilateral electrodes. In other words, contralateral activity obtained over the right hemisphere from left visual field targets was combined with the data from the left hemisphere activity from right visual field targets. From here on, contralateral activity is presented over right hemisphere electrodes and ipsilateral activity over the left hemisphere. Therefore, the analyses reported in the subsequent sections were performed on data that were collapsed across target orientation (horizontal/vertical) and visual field. The statistical output containing all factors, their main effects, and interactions can be found in the Appendix.

Behavior

Target RT (in milliseconds) was analyzed using a 2x2x2 repeated measures ANOVA with Cue Validity (cued or uncued), ISI (short or long), and Congruency (congruent or incongruent) as the main factors. The only significant main effect was for ISI, $F(1,15) = 12.15$, $p = .003$ with short ISI targets (mean = 521ms) being faster than long ISI targets (mean = 534ms). A significant Cue Validity x ISI interaction was found $F(1,15) = 22.3$, $p < .001$. Subsequent planned comparisons revealed that cued targets were responded to significantly faster than uncued targets only at short the ISI. See **Figure 4** for condition means. This was true for both the congruent (short uncued-cued difference = 23.9ms, t(15) =

6.1, p < .001; long uncued-cued difference = -4.8ms, t(15) = -.95, p = .355) and incongruent conditions (short uncued-cued difference = 9.4ms, t(15) = 2.3, p = .036; long uncued-cued difference = -9.1ms, t(15) = 1.91, p = .076. The cueing effect (uncued-cued difference) was larger for congruent with respect to incongruent conditions t(15) = 3.29, p = .005 at the short ISI. Cueing effects were not significantly different between these two conditions at the long ISI t(15) = -.91, p = .379.

Target accuracy was analyzed using the same factors used for RT. A significant main effect of cue validity was obtained $F(1,15) = 20.92$, $p < .001$, with cued targets (mean = 95.4%) responded to more accurately than uncued targets (mean = 94%). There was also a main effect for congruency $F(1,15) = 6.1$, $p = .026$, with incongruent targets (mean = 95.2%) being more accurate than congruent targets (mean = 94.%). No other main effects or interactions were significant all $p > .05$, See **Figure 4**.

Event-related Potentials

The use of ERPs allowed us to assess neural processing of M and P activity from stimulus onset up through the overt behavioral response. This method assures precise temporal resolution of cognitive operations that may not always be present in overt behavior. While most of the hypotheses involving ERPs focused on target processing, it is also important to evaluate the activity generated by cue stimuli. ERPs to cues allowed us to determine if in fact our stimuli were activating the correct visual streams. Analyzing cue ERPs also let us see if the evoked activity to an M or P cue was different when participants were set to respond to either an M or P target.

Cues

Cue-evoked activity was analyzed using a 2x2 ANOVA with Cue Type and Electrode Site (lateral occipital, medial occipital). The latency of the peak P1 amplitude as well as the peak P1 amplitude was calculated over the hemisphere contralateral to stimulus presentation. The latency analysis revealed a significant main effect for Cue Type, $F(1,15) = 15.05$, $p = .001$, with M cues P1 peak amplitude latency (94ms) occurring earlier than the P cue (115.3ms). See **Figure 5**. No other main effects or interactions for the latency analysis were significant. Since the latencies for P and M cues were significantly different, the maximum amplitude for the P1 was calculated using a +/- 10ms window around the mean peak latency obtained from the prior analysis. The P1 maximum amplitude analysis revealed a main effect of Cue Type $F(1,15) = 14.6$, $p = .002$ (Congruent = .57 μv, Incongruent = .23 μv), a main effect of electrode $F(1,15) = 6.42$, $p = .022$ (Lateral = .28 μv, Medial = .52 μv), and a congruency by electrode interaction $F(1,15) = 10.02$, $p = .006$ (larger congruency difference at medial electrode site).

Prior research looking at ERP congruency effects to peripheral cues found an early enhancement to congruent with respect to incongruent cues over frontal electrodes (Arnott et al., 2001). With this in mind, and after initial observation of the data, I analyzed two front/lateral electrodes (**Top of Figure 5**) over a 200-300ms window in a post-hoc analysis to test for congruency differences in the present experiment. This analysis indicated that congruent cues produced a significantly larger early positive component over frontal/lateral electrodes $F(1,15) = 7.58$, $p < .015$. Based on this analysis, and assuming the difference between congruent and incongruent cues is affected by the experimental task, I predicted that congruent cues (M) in Experiment 2 would produce a greater positive potential than incongruent (P) cues.

Target P1

The amplitude of the target-evoked P1 component (80-120ms) was analyzed over contralateral electrode sites using a repeated-measures ANOVA with the factors Cue Validity (cued or uncued) ISI (short or long), Congruency (congruent or incongruent), and Electrode (medial or lateral). The full ANOVA output can be found in the Appendix. The analysis showed a main effect for Cue Validity $F(1,15) = 6.59$, $p = .02$ (cued = 1.4μv, uncued = 1.29μv) and a Cue Validity by Electrode interaction $F(1,15) = 9.21$, $p = .008$. A three way interaction between Cue Validity, ISI, and Electrode was also significant $F(1,15) = 4.69$, $p = .047$. This interaction showed that the cued targets were larger than uncued targets only at the short ISI over the lateral occipital electrode. No other main effects or interactions were significant at $p < .05$. Subsequent planned t-tests demonstrated that the cueing effect at the short ISI over the lateral occipital electrode was present for both congruency conditions. The interaction between Cue Validity and Congruency was not significant $F(1,15) = .10$, $p = .75$. At the short ISI the uncued-cued difference was significant for both the congruent ($t(15) = 4.1$, $p = .001$) and incongruent ($t(15) = 2.47$, $p = .026$) conditions. However, this difference was not statistically significant in the congruent ($t(15) = -..09$, $p = .927$) or incongruent ($t(15) = -.32$, $p = .753$) conditions at the long ISI. See **Figure 6**.

Target IIN

The IIN component was analyzed over ipsilateral electrode sites (200-300ms) with the same factors used in the target P1 analysis. The full ANOVA output can be found in the Appendix**.** A significant main effect for Cue Validity (cued = 1.2μv, uncued = .74μv) and ISI (short = .45μv, long = 1.59μv) was obtained, $F(1,15) = 11.09$, $p = .005$, $F(1,15) = 6.6$, $p = .021$ respectively. The interaction between Cue Validity and ISI was also significant, $F(1,15)$

= 33.4, $p < .001$. Subsequent planned comparisons revealed a significant uncued-cued difference at short ISIs for both congruent (t(15) = 3.6 = p = .002) and incongruent (t(15) = 4.4, p = .001) conditions. This difference was also significant for the congruent condition at the long ISI (t(15) = -2.36, p =..032); however the cued-uncued difference was in the opposite direction compared to the short ISI conditions. That is, the cued targets in the congruent long ISI condition produced a greater negativity compared to the uncued targets in the same condition. The cued-uncued difference was not significant for the incongruent long ISI condition (t(15) = .379, p = .710) . See **Figure 7**.

Target P300

The amplitude of the target-evoked P300 component was analyzed over central-midline/posterior-midline electrode sites using a repeated-measures ANOVA with the factors Cue Validity (cued or uncued) ISI (short or long), Congruency (congruent or incongruent), and Electrode (central versus more posterior). While the P300 is normally analyzed as a unitary component with one time window, the inspection of the topographic voltage maps and ERPs revealed two dominant components over the P300 range we normally analyze (See **Figure 8**)**.** The first component corresponds with the visually-evoked P2, or the second dominant positive deflection in the ERP waveform peaking around 250ms. The P2 is postulated to reflect general stimulus evaluation and is known to be influenced by attention (Crowley and Colrain, 2004, Potts, 2004). Thus, we analyzed the P2 separately from the P300 in both Experiments 1 and 2.

P2

Based on the peak amplitude distributions provided by the topographic voltage maps, the P2 analysis was performed on frontal/central electrodes (190-270ms). This analysis

revealed a significant main effect for Cue Validity $F(1,15) = 15.9$, $p = .001$, (cued = 1.7μv, uncued = 2.4μv), a main effect for ISI $F(1,15) = 6.8$, $p = .02$ (short = 1.5μv, long = 2.5μv). No other significant main effects or interactions were found, $p < .05$. Paired-samples t-tests were used to assess any differences between cued and uncued trials. At the short ISI the uncued-cued difference was not significant for the congruent condition ($t(15) = -1.1$, $p = .286$) but was significant in the incongruent condition ($t(15) = -3.6$, $p = .003$). The cued-uncued difference was also significant at the long ISI for both the congruent ($t(15) = -2.25$, $p = .04$) and incongruent ($t(15) = -3.07$, $p = .008$) conditions. See **Figure 9**.

P300

The P300 analysis (300-500ms) revealed a main effect for Cue Validity $F(1,15) = 51.77$, $p < .001$, (cued = 2.4μv, uncued = 1.9μv), a main effect for ISI $F(1,15) = 16.4$, $p = .001$ (short = 1.9μv, long = 2.4μv), and a main effect for Congruency $F(1,15) = 16.26$, $p < .001$ (congruent = 2.01μv, incongruent = 2.31μv). A two-way interaction was obtained for Cue Validity and ISI $F(1,15) = 30.08$, $p < .001$ (cued larger than uncued only at short ISI), ISI and Congruency $F(1,15) = 15.15$, $p = .001$ (larger short-long ISI difference for congruent than incongruent), Cue Validity and Electrode $F(1,15) = 6.25$, $p = .024$, and ISI and Electrode $F(1,15) = 19.05$, $p < .001$. No other significant main effects or interactions were found, $p < .05$. The interaction between Cue Validity and ISI was probed using planned paired-samples t-tests. At the short ISI the uncued-cued difference was significant for both the congruent ($t(15) = 4.98$, $p < .001$) and incongruent ($t(15) = 5.29$, $p < .001$) conditions. However, this difference was not statistically significant in the congruent ($t(15) = -.96$, $p = .352$) or incongruent ($t(15) = 1.27$, $p = .225$) conditions at the long ISI. See **Figure 10**.

Experiment 1 Discussion

The purpose of Experiment 1 was to evaluate the behavior and neural underpinnings of attentional capture to M or P cue distractors while performing a P target discrimination task. This was assessed by measuring reaction time, accuracy, and ERPs to P-target stimuli preceded by a non-predictive exogenous M or P cue. We predicted that RT would be faster and accuracy better for cued, with respect to uncued target trials. Moreover, the benefit for cued trials was expected to be greater at short ISIs and on congruent trials. The accuracy data partially support this hypothesis showing that cued targets were more accurately identified than uncued targets; however this difference did not significantly change as a function of ISI or Congruency. Overall, incongruent targets were more accurate than congruent targets. It may be the case that regardless of the top-down setting, M-capturing cue stimuli produce better accuracy compared to P-capturing cues due to its faster conduction and reported ability to better activate the involuntary attention system. Previous research has indicated that a peripheral cue consisting of a luminance contrast significantly decreases perceptual thresholds for simple stimulus dimensions such as luminance and orientation on cued compared to uncued trials (Carasco et al., 2004; Steinman et al., 1997). Transient allocation of attention briefly boosts the gain of incoming stimuli at the cued location making a stimulus appear brighter compared to uncued or in neutral conditions when no cue is presented. With this in mind it seems that the M cues may have enhanced perception of subsequent targets, thus increasing their accuracy compared to P cues.

It was predicted that cued targets would have faster RTs than uncued at short ISIs whereas this pattern would be reversed at long ISIs due to IOR. The RT data support the idea that both M and P distractors can capture attention and speed RT to subsequent cued relative to uncued targets even when the primary goal is to respond to a target activating the P stream.

This claim was supported by faster RTs to cued relative to uncued targets for both congruency conditions at the short ISI but not the long ISI. This finding was expected based on previous studies finding behavioral evidence of attentional capture using M and P cue stimuli (e.g. Lu, 2006). The RT data also show that the cueing effect (cued-uncued) was larger on congruent trials compared to incongruent trials at the short ISI. This result indicates that the facilitation effects due to attentional capture are activated to a different degree or possibly by different mechanisms. The top-down settings for P stimuli are more selective to P activation than M. It was predicted that cued targets at the long ISI would be significantly slower when compared to uncued targets at the same interval due to IOR. The data partially support this hypothesis in that RTs are increased on cued relative to uncued trials at the long ISI. However, this trend was not statistically significant for either the congruent or incongruent condition. Though not significant at an alpha level of .05, the cued-uncued RT difference (-9.1ms) in the incongruent condition was close to significance, $p = .07$, with uncued targets responded to faster than cued targets. This finding lends support to the idea that even though participants were engaged to respond to a P target, M stimuli may be more likely to bias early stages of the reflexive system compared to P stimuli (Steinman et al., 1997). It has also been documented that IOR is easier to obtain on detection with respect to discrimination target responses. The lack of significant IOR effects at the long ISI in Experiment 1 may be due to the requirements of the task or to an interval that was not optimal for IOR effects using these stimuli. While overt behavior provides a reliable measure of cognitive functions, the temporal resolution afforded by ERPs enables a precise measurement of mental operations from stimulus onset to the overt response to that stimulus. This may help uncover processing mechanisms that are masked in overt RT.

Since a major goal in the present experiments was to evaluate the mechanisms of reflexive attention engaged by M and P stream activity, it is important that the cue stimuli were indeed activating different visual systems. Based on the cue-evoked activity it is apparent that M and P cues were activating different neuronal populations. This is evidenced by a significantly faster peak P1 latency for M compared to P stimuli over contralateral occipital electrodes. This is consistent with the neural conduction speed of these systems. Not only were the peak P1 latencies different, but so were the maximum amplitudes. P cues evoked a significantly larger P1 compared to M cues again suggesting the cues were activating different visual systems indicative of M and P processing.

Other cue processing characteristics at later stages were in line with congruent stimuli eliciting significantly greater activity over frontal electrodes. As seen in **Figure 4**, anterior electrodes displayed a greater positivity to congruent cues between 200-300ms after stimulus onset. While the processing speed and amplitude of M and P cue stimuli were different at early visual stages, only the amplitude difference was present over frontal electrodes suggesting that when engaged to respond to P targets, M and P cues are processed over frontal electrodes at a similar rate, but congruent cues elicit a greater response due to a match with current goal properties.

ERPs time-locked to targets also support the view that both M and P stream activation initiate reflexive attentional capture. This was evidenced at both early and late stages of processing as indexed by increased P1 and P300 ERP components for cued relative to uncued trials but only at short cue to target intervals. This finding is in line with prior studies showing that early stages of visual processing are reflexively biased by objects triggering an automatic deployment of attention. This automatic biasing has been shown to enhance the P1

component on cued relative to uncued trials at short ISIs regardless of cue/target congruency and independent of cueing effects seen in RT (Hopfinger and Ries, 2005).

The IIN component also revealed evidence of attentional capture to both M and P cues at short ISIs due to the greater negativity to uncued target stimuli over ipsilateral electrodes compared to cued targets. This component is believed to reflect the disengagement or reorienting of attention to the target at short ISIs. If capture to these stimuli was contingent upon cue/target compatibility, then no IIN effect should have occurred in the incongruent condition; however, uncued targets produced a significantly greater negative potential compared to cued targets in the incongruent condition suggesting that incongruent cues also captured attention.

While it is known that the IIN indicates evidence of attentional capture, especially at short ISIs whereby uncued targets elicit a greater negativity than cued targets, it is not entirely clear how or if top-down control settings affect the processing of uncued target trials. It is possible to assess any differences top-down contingencies may had by looking at the difference between the uncued targets for each congruency condition. As seen in Figure 20, cued targets were not different over the ipsilateral electrode location, which showed the original IIN effect. However, the uncued targets produced a longer peak latency on the ipsilateral N1 to congruent targets, which is where the IIN component begins to form. This indicates that congruent cues may have been engaged longer and thus the reorienting to the uncued target was delayed compared to targets preceded by an incongruent cue. To test this, I ran a peak latency analysis on this component with a 150-250ms window and found a significant latency difference between the congruent and incongruent conditions on uncued trials $t(15) = 3.05$, $p = .008$. While this was a post-hoc analysis, it does provide future

researchers valuable insight into the characteristics of the IIN component under different attentional control settings.

Further research will also need to expand on the finding that in the congruent but not incongruent long ISI condition cued rather than uncued targets produced a greater negativity. This was not expected. It is possible that when a target did not appear immediately after a congruent cue subjects were biased to orient to the opposite cue location. This would result in them having to reorient back to the originally cued location on cued trials. Another possibility is that the congruent cues produced a small inhibitory effect specific to attentional reorienting at the cued location on long ISI trials. Since subjects could presumably tell the difference between short and long ISI conditions but not long ISI and catch trial conditions, they may have been less alert to an upcoming target at the long ISI. This would result in greater reorienting behavior to the target since it was not always present.

The findings from the P2 analysis show that uncued targets produced a larger positivity compared to cued trials. The time range of the P2 is similar to the time range used in prior studies evaluating the visual P2 component (180-270ms). This component is generally believed to represent target evaluation and is generally more positive to unattened versus attended stimuli (Martinez et al., 2003; Potts, 2004; Song, Li, Luo, Du, and Ji, 2006, Wang, Jin, Xiao, Fan, and Chen, 1999). Using a visual attention task Song and colleagues (2006) found that the P2 component increased over anterior brain regions as the focus of attention widened. Using Curry software they localized the P2 component to parietal brain areas (left:x=37.5, y=25.5, z=65.9; right: x=30.2, y=61.4, z = 43.7). The distribution of P2 target activity in this experiment is consistent with others showing an anterior distribution at the same time range (Makeig et al., 1999; Song et al., 2006). The present results and

interpretation of the P2 mesh nicely with prior visual attention experiments in that cued, or attended targets, were likely processed with a more constricted focus of attention compared to uncued targets, thus producing a smaller P2 (Song et al., 2006; Talsma et al., 2005).

The target-evoked activity revealed in the P2 was characteristically different from the P300 activity. The P300 in Experiment 1 is consistent with prior research using similar paradigms such that cued targets produced a larger component than uncued trials at the short ISI (Hopfinger and Mangun, 1998, 2001; Hopfinger and Ries, 2005). This finding is likely due to recognition and quick updating of the target relevant information in working memory occurring shortly after the distracting cue stimulus.

To summarize, the results of Experiment 1 indicate attention can be captured and facilitate behavioral and neural processing of P targets preceded by either M or P cues. Each cue type elicited neural activity that was both qualitatively and quantitatively different and in line with prior experiments showing the faster processing speed of the M compared to the P system. While the initial cues produced different neural signatures, they did produce similar attentional benefits. One could argue that the larger target P1 on cued trials is due to the sensory overlap from the preceding cue. If attentional capture had been masked by overlapping activity from the cue onto the target, the P1 to cued targets should have occurred sooner when preceded by an M cue and been larger when preceded by a P cue. However, cued targets exhibited similar activity at both short and long ISIs when preceded by either an M or a P cue. We have seen that top-down control may influence the attention effects observed here. One influence is conveyed by the cued-uncued difference in RTs being larger to P cues than M cues when looking for P targets and a significant delayed onset of the IIN on congruent trials. It is possible that top-down attentional control settings for P stimuli

affect incoming sensory signals differently than M stimuli. Experiment 2 was designed to test if behavioral and neural signatures of attentional capture change when the main task goal focuses on M stream instead of the P stream.

Experiment 2 - M and P cues, M target

Methods

Participants

Participants consisted of 16 (7 females) healthy, right-handed adults (average age 27.9 years) with 20/20 or corrected to 20/20 color vision and were reimbursed $10 per hour for their time.

EEG Recording

EEG Recording was the same as Experiment 1.

Materials and Procedure

In Experiment 2, an M-target image randomly appeared in the middle of one of the placeholders (i.e. in the center of the small box) just prior to target presentation. The interval between the cue and target was either short (12-212ms) as to assess the potential neural enhancements in target processing traditionally seen at this short interval or long (712-912ms) to assess IOR effects. The inter-trial interval was 1200-1500ms. Targets in the second experiment consisted of an M-pathway target with an apparent motion to the left or right. Participants were instructed to make a right/left discrimination response by pressing one button with the right index finger if it was to the left and their right middle finger if it was to the right (see **Figure 11** for an example of the trial sequences). Cue presentation was completely random and in no way indicative of where the subsequent target occurred. Targets appeared in each location with the same probability. This presumably left

participants with little incentive to attend to the cue. Thus, the main manipulations in Experiment 2 were the congruency between the cue and target and cue/target interval or ISI. The M target should have induced subjects to adopt a top-down setting for M stimuli.

Data Analysis

Data Analysis was the same as Experiment 1

Experiment 2 Predictions

Behavior

We expected to find normal reflexive cueing effects where cued targets would elicit significantly faster RTs compared to uncued targets at short ISIs but this effect would reverse at long ISIs due to IOR. Based on previous behavioral data it was also believed that cueing effects would be larger when the cue and target properties are congruent, i.e. M cue/ M target. Overall accuracy was also expected to be better to cued with respect uncued targets.

P1 Short ISI

We expected that the P1 would be enhanced on cued relative to uncued targets over contralateral electrode sites regardless of target type if both M and P cue stimuli produce similar reflexive shifts of attention. However, it is expected that an enhanced P1 will only be found for M targets and not P targets if M cues only capture attention when looking for M targets. Compared to Experiment 1, it was hypothesized that M targets would be processed faster than P targets due to the temporal processing characteristics of the M and P pathways. If this is the case then M target enhancements on cued trials should occur earlier when compared to the same enhancements seen for P targets.

P1 Long ISI

If both M and P cue stimuli produce IOR effects then it follows that the P1 will be reduced or similar to cued relative to uncued targets over contralateral electrode sites regardless of target type. However, if M cues only capture attention when looking for M targets then we expected the difference in P1 amplitude between cued and uncued targets would be smaller for M targets preceded by P cues compared to M cues since attention presumably must be allocated to a feature or location before that feature or location is affected by IOR.

IIN Short ISI

Similar IIN effects were predicted in congruent and incongruent conditions if M and P cues trigger a reflexive shift of attention independent of top-down goals However, if involuntary attentional shifts are moderated by top-down cue/target contingencies, then the IIN is expected to be larger on M cue/M target trials than P cue/M target. That is, the cued-uncued difference will be greater in the congruent compared to the incongruent condition. Based on the evidence in Experiment 1 the M and P cues may trigger a reflexive shift of attention but disengaging from a congruent cue may take longer due to behavioral relevance of the cue-target contingency. If this is the case then the IIN may be delayed to M targets preceded by an M with respect to a P cue.

IIN Long ISI

We hypothesized that the IIN would be absent to targets preceded by either an M or P cue. The IIN is believed to reflect an automatic disengagement of attention from a cue to the sudden appearance of a target in a different location. However, when the interval is increased between the cue and target, attention is able to disengage without reflexively reorienting to a different stimulus. Therefore, if capture is similar to M and P cues regardless of top-down

settings then the IIN should be absent in each case because attention will have disengaged by the time the target appears. However, if IOR is moderated by top-down cue/target contingencies, then the IIN may appear on congruent trials since attention may stay engaged at the cued position longer when the cue matches top-down expectations. IOR may not be developed by the time the target appears on congruent trials; this would result in attention having to disengage and reorient due to the appearance of the subsequent target.

P300 Short ISI

We predicted similar enhancements in the P300 on congruent and incongruent conditions to cued relative to uncued target trials if both M and P cues trigger a reflexive shift of attention independent of top-down goals. Since the P300 is sensitive to recognition and context updating, we believed that the cued/uncued difference would be greater on M cue/M target trials than on P cue/M target trials since M targets in this experiment are only congruent with the M cues.

P300 Long ISI

If M and P cues trigger a reflexive shift of attention independent of top-down goals, we expected similar effects to cued and uncued targets on congruent and incongruent trials. If the P300 is sensitive to top-down goal recognition and context updating then it is expected that the cued/uncued difference would be larger on congruent compared to incongruent trials.

Results Experiment 2

Behavior

Target accuracy was analyzed using a 2x2x2 repeated measures ANOVA with cue validity (cued or uncued) ISI (short or long) and Congruency (congruent or incongruent) as the main factors. A significant main effect of cue validity was obtained $F(1,15) = 8.84$, p

=.009, with cued targets (96.4%) responded to more accurately than uncued targets (92%). There was also a main effect for ISI $F(1,15) = 6.55$, p =.022, with long ISI targets (95.6%) being more accurate than short ISI targets (mean = 93.7%). The two way interaction between Cue Validity and ISI $F(1,15) = 8.3$, p =.011 showed no difference between cued targets at short (96.3%) and long ISI (96.5%), while uncued targets were more accurate at long (94.6%) compared to short (91.1%) ISI. No other main effects or interactions were significant all $p > .05$.

Target RT in milliseconds was analyzed using the same model used above for accuracy. The model revealed a main effect for Cue Validity $F(1,15) = 12.37$, p =.003 (cued = 431.8, uncued = 443.5), a main effect for ISI $F(1,15) = 6.49$, p = .022 (short = 432.6, long = 442.8), and a main effect for congruence $F(1,15) = 10.97$, p =.005 (congruent = 434.7 , incongruent = 440.7) A significant Cue Validity x ISI interaction was found $F(1,15) = 19.68$, $p < .001$. Subsequent planned comparisons revealed that cued targets were responded to significantly faster than uncued targets only at short the ISI. This was true for both the congruent (short uncued-cued difference = 22.15, t(15) = 4.21, p = .001; long uncued-cued difference = 5.8, t(15) = 1.36, p = .194) and incongruent conditions (short uncued-cued difference = 22.6, t(15) = 4.19, p = .001; long uncued-cued difference = -3.6, t(15) = -1.06, p = .305. See **Figure 12**.

ERPs

Cues

Cue-evoked activity was analyzed using a 2x2 ANOVA with Congruency and Electrode Site (lateral occipital, medial occipital). The latency of the peak P1 amplitude as well as the peak P1 amplitude was calculated over the hemisphere contralateral to stimulus

presentation. The latency analysis revealed a significant main effect for congruency, $F(1,15) = 69.51$, $p < .001$, with congruent (M) P1 peak amplitude latency (96.5ms) occurring earlier than its incongruent (P) counterpart (119ms). See **Figure 13**. No other main effects or interactions for the latency analysis or maximum amplitude were significant, all $p < .05$.

Based on the findings from Experiment 1, cue activity in Experiment 2 was analyzed over the same frontal electrodes showing a larger positivity to congruent with respect to incongruent stimuli. Keep in mind that congruent cues in Experiment 2 primarily stimulated the M stream while in Experiment 1 they stimulated the P stream. The present analysis also showed a significant positive enhancement to congruent cues compared to incongruent cues $F(1,15) = 5.16$, $p = .038$. Interestingly the congruent cue peaked earlier than the incongruent cue. This was not the case in the first experiment where only a significant amplitude difference was obtained. These findings indicate that while early sensory components are consistent with the neural conduction speed of M and P streams in both experiments, later ERP components show significantly larger positive potentials to congruent stimuli and peak latency differences are only present when top-down goals are set to respond to M stream stimulation.

Target P1

The amplitude of the target-evoked P1 component (75-115ms) was analyzed over contralateral electrode sites using a repeated-measures ANOVA with the factors Cue Validity (cued or uncued) ISI (short or long), Congruency (congruent or incongruent), and Electrode (medial or lateral). The full ANOVA output is located in the Appendix**.** The analysis showed a main effect for Cue Validity $F(1,15) = 12.25$, $p = .003$ (cued = .42μv, uncued = .08μv), ISI $F(1,15) = 4.85$, $p = .043$ (short = .56μv, long = .07μv), and Congruency $F(1,15) = 6.23$, $p =$

.025 (congruent = .35μv, incongruent = .14μv). Significant two-way interactions were obtained between Cue Validity and ISI $F(1,15) = 13.78$, $p = .002$, ISI and Congruency $F(1,15) = 7.37$, $p = .02$, and Congruency and Electrode $F(1,15) = 20.14$, $p < .001$. A three-way interaction between ISI, Congruency and Electrode was also found $F(1,15) = 10.66$, $p = .005$. No other main effects or interactions were significant at $p < .05$. In line with the predictions for this experiment, we probed the two-way interaction between Cue Validity and ISI using paired-samples t-tests. At the short ISI the cued-uncued difference was significant for both the congruent (difference = .67μv, $t(15) = 5.42$, $p < .001$) and incongruent (difference = .59μv, $t(15) = 2.87$, $p = .012$) conditions. However, this difference was not statistically significant in the congruent (difference -.03μv, $t(15) = -.357$, $p = .726$) or incongruent (difference = .14μv, $t(15) = 1.25$, $p = .231$) conditions at the long ISI. See **Figure 14**.

Target IIN

The IIN component (200-300ms) was analyzed over ipsilateral electrode sites with the same factors used in the target P1 analysis. The full ANOVA output can be found in the Appendix**.** A significant main effect for Cue Validity (cued = .84μv, uncued = .6μv) was obtained, $F(1,15) = 14.74$, $p = .012$. The interaction between Cue Validity and ISI was also significant, $F(1,15) = 22.53$, $p < .001$. (cued/short = .87μv, cued/long = .81μv, uncued/short = .23μv, uncued/long = .97μv). Other two-way interactions included ISI and Congruency $F(1,15) = 5.22$, $p = .037$ (short/congruent = .5μv, short/incongruent = .6μv, long/congruent = .96μv, long/incongruent = .82μv). There was also a significant three-way interaction between Cue Validity, ISI, and Congruency, $F(1,15) = 7.41$, $p = .016$. Subsequent planned comparisons revealed a significant cued-uncued difference at short ISIs for both congruent

(difference = .52μv, t(15) = 2.9 = p =.01) and incongruent (difference = .75μv, t(15) = 5.61, p <.001) conditions. This difference was not significant at the long ISI in the congruent condition (difference = -.08μv, t(15) = -.27, p =.374) but was significant in the incongruent condition (difference = -.25μv, t(15) = -2.66, p = .018). See **Figure 15**.

P2

The P2 was analyzed using the same factors as those used in the IIN analysis. The P2 analysis (180-250ms) showed a significant main effect for ISI, $F(1,15) = 28.76$, $p < .001$, (short = 2.5μv, long = 3.8μv) and a significant Cue Validity, ISI, Congruency interaction $F(1,15) = 8.37$, $p = .011$. No other significant main effects or interactions were found, $p < .05$. Planned paired-samples t-tests were used to assess any differences between cued and uncued trials. At the short ISI the uncued-cued difference was significant for the congruent condition (t(15) = -3.39μv, p = .004) but was not significant in the incongruent condition (t(15) = -.42, p = .677). The cued-uncued difference was also significant at the long ISI for the congruent condition (t(15) = -2.16, p = .047) but not the incongruent condition (t(15) = -1.51, p = .151). See **Figures 16 and 17**.

P300

The amplitude of the target-evoked P300 component (300-500ms) was analyzed over central-midline/posterior-midline electrode sites using a repeated-measures ANOVA with the factors Cue Validity (cued or uncued) ISI (short or long), Congruency (congruent or incongruent), and Electrode (central versus more posterior). The full ANOVA output can be found in the Appendix. This analysis revealed a main effect for Cue Validity $F(1,15) = 36.19$, $p < .001$, (cued = 2.59μv, uncued = 1.89μv), and a main effect for ISI $F(1,15) = 32.92$, $p < .001$ (short = 1.79μv, long = 2.69μv). A two-way interaction was obtained for ISI and

Congruency $F(1,15) = 13.16$, $p = .003$ (short congruent (1.59μv), short incongruent (1.97μv), long congruent (2.83μv), long incongruent (2.56μv)), and for ISI and Electrode $F(1,15) = 20.22$, $p < .001$. No other significant main effects or interactions were found, $p < .05$. See **Figure 18**.

Experiment 2 Discussion

Similar to the behavioral results in Experiment 1 and replicating behavioral results of prior M and P peripheral cueing studies, accuracy was significantly better and RT significantly faster on cued with respect to uncued trials. This indicates that overall, attention was captured to the cued location and enhanced response time and also increased perceptual target discrimination compared to uncued trials. The main effect for ISI and the Cue Validity x ISI interaction suggests that at short ISIs uncued trials may suffer a cost in performance due to attention being engaged at the location of the cue. This is possible since cued trials did not differ in accuracy in at either ISI but the uncued trials at short ISI were significantly worse than those at the long ISI. Having a neutral condition that was neither cued nor uncued and overall alertness effects were kept constant across conditions would enable one to better estimate the attentional effects of enhancement or inhibition. Again, it is important to consider the cognitive processing that occurs prior to overt behavior in order to get better understanding of the mechanisms underlying attentional capture.

Further evidence that both the M and P cues captured attention independent from top-down control comes from the significantly larger P1 on cued relative to uncued trials at short ISIs only in both congruent and incongruent conditions. The long ISI condition did not show any significant differences in P1 amplitude on cued or uncued trials. It is possible that the task used in this experiment induced a top-down goal state that prevented IOR from

occurring. The difference between cued and uncued P1 target amplitudes at short ISIs did not differ based on the congruency between the cue and target. This implies that top-down attentional control settings for M dominant stimuli do not interact with cue validity at early levels of processing. However, when only looking at the P1 for cued targets between contingency groups, it is evident that while the cued activity does not differ at the long ISI between congruent and incongruent targets, the P1 on cued congruent trials is significantly larger than the P1 on cued incongruent trials (See **Figure 21**). This suggests that while both M and P cues capture attention at short ISIs, top-down attentional control settings for M stimuli are able to disengage from incongruent cues more quickly than congruent cues or that these settings increase the neural biasing for congruent stimuli.

In line with Experiment 1 and prior ERP studies examining attentional capture at short ISIs, the IIN component was significantly more negative going for uncued compared to cued trials. The significant interaction between Cue Validity and ISI indicates the increased negativity on uncued trials occurred to both congruent and incongruent targets but only at the short cue/target interval. If attention was not captured by either cue or if attention had time to disengage prior to target appearance then cued and uncued targets should show similar amplitudes over ipsilateral, occipital electrodes. It does not appear that the IIN effect is completely contingent upon the congruency between the cue and target, for the difference between cued and uncued targets was significant in each condition at the short ISI. However, it is possible to assess any differences top-down contingencies may have had by looking at the difference between the uncued targets for each congruency condition as in Experiment 1. As seen in **Figure 21**, cued targets were not different over the ipsilateral electrode location showing the original IIN effect. However, uncued congruent targets peaked later on the

ipsilateral N1 compared to uncued incongruent trials. This is similar to what we found in Experiment 1. This suggests that congruent cues may have been engaged longer and thus the reorienting to the uncued target was delayed compared to targets preceded by an incongruent cue.

As in Experiment 1, uncued targets elicited a larger P2 when compared to cued targets. However, this was only true for congruent targets for both short and long ISIs. Given the general function reflected in the anterior P2, this finding implies that congruent cues produced a more narrow focus of attention when evaluating targets compared to incongruent cues. Overall, the P2 was larger at long with respect to short ISIs, which is also consistent with more attentional focus or enhanced target evaluation at short cue to target intervals. At long cue/target intervals, attention is presumably not as engaged as it is at short intervals.

The target-evoked P300 was larger on cued compared to uncued trials at both ISIs and congruency conditions. While we expected this finding at the short ISI, we were surprised to see the cued-uncued difference still apparent at the long ISI. One explanation for this finding is that the context updating function reflected in the P3 remains active longer when looking for M compared to P stimuli. Further discussion of the P300 in Experiments 1 and 2 is presented below.

The results from Experiment 2, like Experiment 1, provide direct evidence that both M and P activation can trigger a reflexive shift of attention and enhance early visual processing and later higher-order functioning. This was evidence by faster target RTs, larger P1 target amplitude, and significant IIN effects to cued targets at short but not long ISIs in both the M and P conditions. However, the results from the current experiment demonstrate that top-down settings for an M stimulus affect target processing differently than top-down

settings for a P stimulus, even when both stimuli are preceded by identical events. Further similarities and differences between experiments are discussed below.

General Conclusions

Our visual system has evolved attentional functions to prioritize only a small fraction of the available visual input. Priority to attentional processing resources is influenced by both bottom-up and top-down mechanisms; however, there are instances when one of these mechanisms is dominant and the other has little influence on stimulus selection. The abrupt appearance of a new object, luminance transient or sudden movement can trigger automatic attentional orienting primarily through bottom-up processing mechanisms. It is believed that the underlying visual pathway that encodes luminance contrast and motion, the M pathway, is responsible for reflexive shifts of attention. Recently, however, behavioral evidence suggests that the P pathway, which is not sensitive to these stimulus attributes, can also trigger reflexive shifts of attention. Our results support the hypothesis that both M and P processing streams can independently trigger reflexive attention mechanisms in the brain.

Processing of the cue stimuli in both experiments shows that M cues had a shorter P1 peak latency than P cues, but P cues had larger P1 amplitudes. Directly comparing the cue processing between experiments shows that top-down settings may bias early visual areas. While the difference was not statistically significant over contralateral electrodes, the peak amplitude of the P1 between Experiment 1 and Experiment 2 was enhanced for cues activating the M stream when looking for M targets relative to P targets. P cues on the other hand did not show this difference. As seen in **Figure 19**, the amplitude of the P1 to M cues when looking for M targets was larger than the P1 amplitude evoked by the same stimulus when looking for a P target. However, the P1 amplitude for P cues did not differ based on

target type. The latency of the P1 peak did not did not differ between M and P cues when target response requirements changed. This finding implies that top-down settings for M-type stimuli may bias early visual activity prior to their appearance while top-down settings for P-type stimuli may not. This finding my insinuate that more pronounced attention effects would be observed to M targets preceded by M cues due to the larger evoked P1 for congruent M cues. If P1 amplitude is indicative of attentional capture, it is reasonable to assume from the data that the threshold of activation necessary to trigger a reflexive shift was exceeded by all cues. In other words, engaging the reflexive attention network may be an all or nothing phenomenon, such that once a certain amount of activation is present, attention is allocated. In this case, both small and larger activations would trigger similar shifts of attention. However, the P1 activity alone may not be the only contributor to reflexive attentional allocation.

Further evidence that top-down goals differentially affected processing of the same M and P cues between experiments is observed in the peak latency differences in cue processing over anterior electrode sites. In Experiment 1 when the primary target goal required a response to a P targeting stimulus only the amplitude differed between M and P cues, while in Experiment 2 when subjects responded to M targets both the amplitude and peak latency were influenced. In each experiment, congruent cues produced larger potentials than incongruent cues. This finding supports the idea that both the processing speed and overall magnitude of the same stimulus changes as a function of its relation to current task goals focusing on either the M or P processing stream.

Cue Validity for the target-evoked P1 did not interact with electrode location in Experiment 2 as Experiment 1 did. In other words, more electrodes displayed cued-ucued

differences to M versus P targets. This suggests that the overall cueing effect was more spatially pronounced in Experiment 2 possibly due to the effectiveness of the M stream in attentional capture or due to more neural populations sensitive to this effect. Another possible explanation for this finding is that ventral activation produced by the P targets in Experiment 1 was generated by neurons oriented differently from those activated by an M target. For example, it is theoretically possible that both experiments produced similar cueing effects but neurons sensitive to these effects in the P stream generated activity in brain regions that were not oriented to the scalp in the same fashion as those activated by M stream.

When comparing the differences in the peak latency of the target P1 between experiments it is evident that M targets in Experiment 2 peaked sooner than the P targets used in Experiment 1. This finding corroborates earlier findings obtained from piloting and indicates that our stimuli manipulations primarily activated the parvocellular and magnocellular streams in Experiments 1 and 2 respectively.

Further support that our stimuli activated the P or M stream comes from the accuracy and RT data. Overall reaction times for the M targets were much faster than P targets. M targets were processes sooner or more quickly than P targets (See **Figure 22**). One could argue that since the tasks are not the same, the RT differences between experiments are not reliable. While the behavioral task was technically different between Experiments 1 and 2 (discriminating horizontal from vertical in Experiment 1, and right versus left in Experiment 2), each experiment required one of two simple, sensory-discrimination responses that was relatively easy when looking at the error rates. In fact the higher error rates in Experiment 2 suggest that this task may have been more difficult than the task in Experiment 1. If that was the case, then RTs would also be expected to be higher, given of course that there was more

incentive to respond more quickly instead of accurately in Experiment 2 but not in Experiment 1, i.e. speed/accuracy tradeoffs.

The lack of significant IOR findings in the behavioral data may have been due to attention not completely reorienting away from the cue at long ISIs. A theory of IOR function posits that attention is prevented from returning to recently attended locations or features. Since there was nothing to attract the subjects' attention away from the cue, it may have been easier to return to the cued location. Researchers have found IOR effects more frequently when a second cue stimulus is presented shortly after the first but before the target (Posner, 1980; Prime and Ward, 2006). This is done to pull attention back to fixation or away from the first cued location.

The P2 findings in both Experiments 1 and 2 revealed a general trend showing a larger P2 on uncued compared to cued trials. The function of the anteriorally distributed P2 reflects general stimulus evaluation (Potts, 2004). Others have found larger P2 peak (240ms) amplitudes to unattended compared to attended stimuli when attention was voluntarily engaged (Makeig, Westerfield, Townsend, Jung, Courchesne and Sejnowski, 1999; Talsma, Slagter, Nieuwenhuis, Hage, and Kok, 2005). Furthermore, the amplitude of the visually-evoked P2 was larger when participants had a wide or 'zoomed out' focus of attention compared to when the focus of attention was more concentrated or 'zoomed in' (Song et al., 2006). These results all suggest that attended stimuli elicit a smaller P2 component compared to unattended stimuli and this difference may increase as the focus of attention narrows.

There is still not a clear link between the magnitude of the visually-evoked P2 and the primary activation of the dorsal or ventral visual stream. Luck and Hillyard (1994) found a larger P2 to color compared to orientation pop-out targets. However, a different ERP study

found a larger P2 to orientation targets compared to colored targets (O'Donnell, Swearer, Smith, Hokama, and McCarley, 1997). Assuming color and orientation targets triggered the P and M streams respectively based on their feature sensitivity, future studies should try using other stimuli such as motion or high spatial frequencies to activate the M and P streams respectively.

In the present experiments reflexively attended targets elicited a smaller P2 with respect to uncued targets. While it is tempting to interpret this finding as similar to that found to voluntarily attended targets, the topographies of the P2 are different between and within reflexive/voluntary comparisons. For example, sustained voluntary attention in the peripheral visual field elicited an anterior P2 target distribution generated from parietal cortex, while voluntary attention directed by informative cues presented at fixation evoked a more posterior distribution reflective of visual cortical generation (Makeig et al., 1999; Talsma et al., 2005). The targets in the present experiments produced activation over anterior electrodes suggesting a potential parietal generator.

While the interaction between Cue Validity and ISI was not statistically significant for the P300, it did approach statistical significance $F(1,15) = 3.42$, $p = .08$. Based on the ERPs and topographical voltage maps to time-locked targets in Experiment 2, cued targets at the long ISI produced larger amplitudes than the uncued targets in both congruency conditions. This suggests that late stages of processing may still be enhanced when attention is automatically engaged by M or P stream activation, but only when looking for M targets.

It is still unclear what if any effect the koniocellular (K) system had in engaging reflexive attention in the present studies. The K stream, like the M stream, has a fast conduction speed, which would also likely show faster sensory processing compared to P

targeting stimuli. However, the main manipulations in the current studies were designed to primarily target either the M or P pathway. Future research will need to design stimuli to specifically target the K stream such as those activating blue-on cells and compare the evoked activity from M, P, and K activation in order to assess the unique contributions from these streams on reflexive attention (Callaway, 2005).

We developed multiple stimuli targeting either the M or P pathway. Our electrophysiological findings closely resembled those found in previous studies employing similar manipulations. The M and P stimuli showing the greatest disparity were used as peripheral cues in four ERP experiments assessing the effectiveness of M or P stream activation in triggering reflexive shifts of attention. The present experiments highlight the mechanisms of reflexive attention at both early and late stages of processing when triggered by an M or P-targeting stimulus. In addition, we were able to evaluate the influence of prior target knowledge on attentional orienting and found that early sensory processing of the cue stimuli were similar across the two experiments but may have a larger bias for stimuli targeting the M stream.

Both M and P stream activation provided evidence of reflexive capture. This was revealed by decrease RTs to cued compared to uncued targets at the short ISI in both experiments. Moreover, at the same ISI cued targets elicited a significantly larger P1 and late P300 ERP when compared to uncued trials. Further evidence that both M and P stimuli can capture visual comes from the larger negative potentials generated by uncued targets with respect to cued targets in both congruent and incongruent conditions at the short but not long ISI. While each cue type captured attention and enhanced behavioral performance and neural activation, the difference in the onset of the IIN component between Experiment 1 and 2

suggests that congruent cues may have been dwelled upon longer or reorienting from them took more time when compared to incongruent cues. Overall, the results of Experiments 1 and 2 indicate that both M and P stream activation can trigger a reflexive shift of attention but attention effects at the neural level occur earlier and elicit faster behavioral responses for M stream compared to P stream activation. Future work should continue to pursue the underlying neural generators of the components (e.g. IIN, P2) underlying the attentional effects found in the present research.

Future Directions

The findings from the present experiments promise exciting future research opportunities and applications. Many exogenous cueing paradigms present peripheral cues that are non-predictive of the subsequent target of importance. However, in our everyday experiences a sudden change in the environment or the abrupt appearance or movement of an object requires immediate attention to that location. More often than not the location of attentional capture is predictive of future action at that location. For example, when a deer suddenly darts in front of our car while driving home, we usually remain engaged to the location of the deer because we know from experience that more deer are likely to cross in the same place shortly after. Other times, such as in urban combat, orienting attention and remaining engaged to every sudden movement or noise would be counterproductive. Reorienting away from the initial locus of capture is also important. The brain mechanism involved in remaining engaged or reorienting after initial capture can be assessed by varying the predictive validity of the exogenous cue prior to its appearance or presenting exogenous cues that contain task relevant information that is interpreted after its presentation.

Appendix I: Target RTs in Experiment 1

FACTORS

A) Cue Validity	1) Cued	2) Uncued	
B) ISI	1) Short	2) Long	
C) Congruency	1) Congruent	2) Incongruent	
D) Visual Field	1) Right	2) Left	
E) Orientation	1) Horizontal	2) Vertical	

* p < .05

ANALYSIS OF VARIANCE TABLE

SOURCE	SS	DF	MS	F	p
A	3006.24	1	3006.24	2.77	0.1169
AS	16287.91	15	1085.86		
B	21226.64	1	21226.64	12.15	0.0033*
BS	26216.07	15	1747.74		
AB	17830.76	1	17830.76	22.33	0.0003*
ABS	11976.20	15	798.41		
C	2889.08	1	2889.08	2.90	0.1091
CS	14937.75	15	995.85		
AC	2867.83	1	2867.83	14.66	0.0016*
ACS	2933.47	15	195.56		
BC	1700.35	1	1700.35	2.70	0.1213
BCS	9453.46	15	630.23		
ABC	838.22	1	838.22	1.72	0.2094
ABCS	7309.08	15	487.27		
D	17177.51	1	17177.51	7.70	0.0142*
DS	33477.51	15	2231.83		
AD	584.61	1	584.61	0.82	0.3792
ADS	10680.31	15	712.02		

```
BD        448.21  1   448.21   1.17  0.2973
BDS       5765.94  15   384.40

ABD        7.13  1    7.13   0.01  0.9263
ABDS      12071.77  15   804.78

CD       1828.37  1  1828.37   6.01  0.0270*
CDS       4562.95  15   304.20

ACD       519.59  1   519.59   1.39  0.2575
ACDS      5624.37  15   374.96

BCD       926.63  1   926.63   1.55  0.2327
BCDS      8985.77  15   599.05

ABCD       419.98  1   419.98   1.45  0.2474
ABCDS      4349.67  15   289.98

E         48.75  1   48.75   0.01  0.9377
ES      115942.83  15  7729.52

AE       4395.70  1  4395.70   7.09  0.0178*
AES       9303.02  15   620.20

BE       2420.74  1  2420.74   3.39  0.0855
BES      10713.34  15   714.22

ABE       125.29  1   125.29   0.25  0.6253

ABES      7561.26  15   504.08

CE       2023.83  1  2023.83   3.49  0.0816
CES       8710.32  15   580.69

ACE        1.05  1    1.05   0.00# 0.9556
ACES      4926.20  15   328.41

BCE        2.22  1    2.22   0.00# 0.9632
BCES      15105.19  15  1007.01

ABCE      5345.66  1  5345.66  13.57  0.0022*
ABCES      5909.29  15   393.95

DE       45196.24  1  45196.24  14.76  0.0016*
DES      45922.49  15  3061.50

ADE       1395.22  1  1395.22   2.70  0.1213
ADES      7757.54  15   517.17

BDE        1.55  1    1.55   0.00# 0.9514
BDES      6077.85  15   405.19

ABDE       489.93  1   489.93   0.64  0.4374
ABDES     11545.66  15   769.71

CDE        45.64  1   45.64   0.07  0.8017
CDES      10477.86  15   698.52
```

```
ACDE       454.83  1   454.83   1.26  0.2798
ACDES      5427.18  15   361.81

BCDE       14.99  1   14.99   0.08  0.7827
BCDES      2852.64  15   190.18

ABCDE       54.25  1   54.25   0.12  0.7301
ABCDES     6587.86  15   439.19
```

Appendix II: P1 Maximum Amplitude in Experiment 1 (80-120ms)

FACTORS

```
A) Cue Validity    1) Cued     2) Uncued
B) ISI             1) Short    2) Long
C) Congruency      1) Cong     2) Incong
D) Visual Field    1) Right    2) Left
E) Electrode       1) Lateral  2) Medial

   * p < .05
```

ANALYSIS OF VARIANCE TABLE

SOURCE	SS	DF	MS	F	p
A	2.12	1	2.12	6.47	0.0225*
AS	4.91	15	0.33		
B	2.93	1	2.93	1.74	0.2075
BS	25.30	15	1.69		
AB	5.19	1	5.19	3.09	0.0992
ABS	25.23	15	1.68		
C	1.83	1	1.83	3.81	0.0699
CS	7.21	15	0.48		
AC	0.03	1	0.03	0.10	0.7570
ACS	4.84	15	0.32		
BC	0.04	1	0.04	0.04	0.8372
BCS	12.33	15	0.82		
ABC	0.00	1	0.00	0.00#	0.9752
ABCS	3.59	15	0.24		
D	10.06	1	10.06	1.14	0.3020
DS	132.06	15	8.80		
AD	0.00	1	0.00	0.02	0.9024
ADS	4.53	15	0.30		
BD	9.12	1	9.12	5.39	0.0348*
BDS	25.42	15	1.69		
ABD	0.29	1	0.29	0.58	0.4581

ABDS	7.46	15	0.50		
CD	1.53	1	1.53	4.34	0.0547
CDS	5.28	15	0.35		
ACD	0.40	1	0.40	0.97	0.3404
ACDS	6.19	15	0.41		
BCD	0.35	1	0.35	1.24	0.2832
BCDS	4.29	15	0.29		
ABCD	0.06	1	0.06	0.10	0.7550
ABCDS	8.94	15	0.60		
E	22.43	1	22.43	5.40	0.0346*
ES	62.36	15	4.16		
AE	1.83	1	1.83	9.32	0.0080*
AES	2.94	15	0.20		
BE	0.01	1	0.01	0.02	0.8948
BES	7.22	15	0.48		
ABE	0.54	1	0.54	4.63	0.0482*
ABES	1.76	15	0.12		
CE	0.87	1	0.87	11.30	0.0043*
CES	1.15	15	0.08		
ACE	0.00	1	0.00	0.01	0.9251
ACES	1.12	15	0.07		
BCE	0.40	1	0.40	8.96	0.0091*
BCES	0.67	15	0.04		
ABCE	0.01	1	0.01	0.65	0.4325
ABCES	0.35	15	0.02		
DE	4.08	1	4.08	3.89	0.0672
DES	15.74	15	1.05		
ADE	0.21	1	0.21	2.57	0.1298
ADES	1.24	15	0.08		
BDE	0.77	1	0.77	3.01	0.1034
BDES	3.84	15	0.26		
ABDE	0.01	1	0.01	0.27	0.6134
ABDES	0.81	15	0.05		
CDE	0.01	1	0.01	0.32	0.5776
CDES	0.47	15	0.03		
ACDE	0.07	1	0.07	0.72	0.4099
ACDES	1.47	15	0.10		
BCDE	0.19	1	0.19	4.23	0.0576

BCDES	0.68	15	0.05		
ABCDE	0.01	1	0.01	0.37	0.5534
ABCDES	0.47	15	0.03		

Appendix III: IIN Maximum Amplitude in Experiment 1 (200-300ms)

FACTORS

```
A) Cuedness       1) Cued      2) Uncued
B) ISI            1) Short     2) Long
C) Congruency     1) Cong      2) Incong
D) Visual Field   1) Right     2) Left
E) Electrode      1) Medial    2) Lateral
```

* p < .05

ANALYSIS OF VARIANCE TABLE

SOURCE	SS	DF	MS	F	p
A	8.65	1	8.65	11.05	0.0046*
AS	11.74	15	0.78		
B	21.71	1	21.71	6.66	0.0209*
BS	48.91	15	3.26		
AB	14.42	1	14.42	33.17	0.0000*
ABS	6.52	15	0.43		
C	0.20	1	0.20	0.33	0.5743
CS	9.08	15	0.61		
AC	0.91	1	0.91	2.53	0.1324
ACS	5.36	15	0.36		
BC	0.04	1	0.04	0.21	0.6513
BCS	2.80	15	0.19		
ABC	0.14	1	0.14	0.33	0.5733
ABCS	6.37	15	0.42		
D	21.11	1	21.11	4.19	0.0587
DS	75.64	15	5.04		
AD	0.10	1	0.10	0.18	0.6806
ADS	8.12	15	0.54		
BD	0.04	1	0.04	0.03	0.8712
BDS	19.99	15	1.33		
ABD	0.04	1	0.04	0.22	0.6430
ABDS	2.45	15	0.16		

CD	0.02	1	0.02	0.03	0.8653
CDS	10.39	15	0.69		
ACD	0.03	1	0.03	0.10	0.7552
ACDS	4.63	15	0.31		
BCD	0.17	1	0.17	0.39	0.5419
BCDS	6.55	15	0.44		
ABCD	0.33	1	0.33	2.42	0.1409
ABCDS	2.06	15	0.14		
E	104.84	1	104.84	41.14	0.0000*
ES	38.23	15	2.55		
AE	0.02	1	0.02	0.23	0.6355
AES	1.21	15	0.08		
BE	3.65	1	3.65	9.36	0.0079*
BES	5.84	15	0.39		
ABE	0.20	1	0.20	2.79	0.1157
ABES	1.09	15	0.07		
CE	0.30	1	0.30	2.10	0.1681
CES	2.15	15	0.14		
ACE	0.02	1	0.02	0.36	0.5592
ACES	0.70	15	0.05		
BCE	0.19	1	0.19	4.54	0.0500
BCES	0.63	15	0.04		
ABCE	0.15	1	0.15	4.51	0.0507
ABCES	0.50	15	0.03		
DE	2.58	1	2.58	5.34	0.0354*
DES	7.25	15	0.48		
ADE	0.10	1	0.10	2.24	0.1554
ADES	0.67	15	0.04		
BDE	0.38	1	0.38	2.68	0.1224
BDES	2.13	15	0.14		
ABDE	0.11	1	0.11	2.56	0.1304
ABDES	0.67	15	0.04		
CDE	0.00	1	0.00	0.09	0.7649
CDES	0.42	15	0.03		
ACDE	0.00	1	0.00	0.01	0.9100
ACDES	1.18	15	0.08		
BCDE	0.04	1	0.04	0.99	0.3345
BCDES	0.53	15	0.04		

```
ABCDE       0.00  1    0.00   0.00# 0.9556
ABCDES       0.40  15    0.03
```

Appendix IV: P2 Maximum Amplitude in Experiment 1 (190-270ms)

FACTORS

A)	Cue Validity	1) Cued	2) Uncued	
B)	ISI	1) Short	2) Long	
C)	Congruency	1) Cong	2) Incong	
D)	Electrode	1) Central Anterior	2) Central	

* p < .05

ANALYSIS OF VARIANCE TABLE

SOURCE	SS	DF	MS	F	p
A	24.65	1	24.65	15.54	0.0013*
AS	23.79	15	1.59		
B	62.38	1	62.38	6.81	0.0197*
BS	137.46	15	9.16		
AB	0.28	1	0.28	0.28	0.6024
ABS	14.99	15	1.00		
C	2.00	1	2.00	1.26	0.2791
CS	23.76	15	1.58		
AC	3.21	1	3.21	3.81	0.0700
ACS	12.65	15	0.84		
BC	1.01	1	1.01	1.53	0.2355
BCS	9.96	15	0.66		
ABC	2.03	1	2.03	3.86	0.0683
ABCS	7.89	15	0.53		
D	0.61	1	0.61	0.80	0.3840
DS	11.33	15	0.76		
AD	0.00	1	0.00	0.06	0.8087
ADS	0.31	15	0.02		
BD	0.02	1	0.02	0.16	0.6992
BDS	2.34	15	0.16		
ABD	0.00	1	0.00	0.02	0.9018
ABDS	0.31	15	0.02		
CD	0.51	1	0.51	17.54	0.0008*
CDS	0.44	15	0.03		
ACD	0.13	1	0.13	6.44	0.0228*
ACDS	0.31	15	0.02		
BCD	0.12	1	0.12	5.93	0.0278*
BCDS	0.29	15	0.02		

ABCD	0.01	1	0.01	0.83	0.3777
ABCDS	0.10	15	0.01		

Appendix V: P300 Maximum Amplitude in Experiment 1 (300-500ms)

FACTORS

```
 A) Cue Validity    1) Cued             2) Uncued
 B) ISI             1) Short            2) Long
 C) Congruency      1) Cong             2) Incong
 D) Visual Field    1) Right            2) Left
 E) Electrode       1) Midline Center   2) Central Posterior
```

* p < .05

ANALYSIS OF VARIANCE TABLE

SOURCE	SS	DF	MS	F	p
A	21.11	1	21.11	33.11	0.0000*
AS	9.57	15	0.64		
B	6.53	1	6.53	2.56	0.1303
BS	38.21	15	2.55		
AB	19.86	1	19.86	27.55	0.0001*
ABS	10.81	15	0.72		
C	11.76	1	11.76	17.38	0.0008*
CS	10.15	15	0.68		
AC	0.37	1	0.37	0.38	0.5479
ACS	14.87	15	0.99		
BC	21.51	1	21.51	15.17	0.0014*
BCS	21.28	15	1.42		
ABC	1.21	1	1.21	2.84	0.1127
ABCS	6.41	15	0.43		
D	1.04	1	1.04	1.94	0.1838
DS	8.07	15	0.54		
AD	0.04	1	0.04	0.15	0.7048
ADS	4.40	15	0.29		
BD	0.30	1	0.30	0.45	0.5134
BDS	10.13	15	0.68		
ABD	0.41	1	0.41	0.85	0.3714
ABDS	7.32	15	0.49		
CD	0.37	1	0.37	0.88	0.3636
CDS	6.34	15	0.42		
ACD	0.04	1	0.04	0.06	0.8098
ACDS	8.81	15	0.59		
BCD	0.06	1	0.06	0.18	0.6781

BCDS	5.07	15	0.34		
ABCD	0.02	1	0.02	0.04	0.8525
ABCDS	8.23	15	0.55		
E	27.14	1	27.14	16.70	0.0010*
ES	24.38	15	1.63		
AE	0.25	1	0.25	11.74	0.0037*
AES	0.32	15	0.02		
BE	3.13	1	3.13	35.11	0.0000*
BES	1.34	15	0.09		
ABE	0.01	1	0.01	0.47	0.5020
ABES	0.26	15	0.02		
CE	0.00	1	0.00	0.09	0.7727
CES	0.43	15	0.03		
ACE	0.01	1	0.01	2.44	0.1394
ACES	0.08	15	0.01		
BCE	0.01	1	0.01	0.85	0.3718
BCES	0.16	15	0.01		
ABCE	0.09	1	0.09	7.34	0.0162*
ABCES	0.18	15	0.01		
DE	0.08	1	0.08	3.82	0.0697
DES	0.33	15	0.02		
ADE	0.00	1	0.00	0.12	0.7358
ADES	0.49	15	0.03		
BDE	0.00	1	0.00	0.08	0.7852
BDES	0.28	15	0.02		
ABDE	0.09	1	0.09	7.41	0.0157*
ABDES	0.17	15	0.01		
CDE	0.00	1	0.00	0.83	0.3763
CDES	0.05	15	0.00		
ACDE	0.00	1	0.00	0.19	0.6658
ACDES	0.34	15	0.02		
BCDE	0.00	1	0.00	0.03	0.8572
BCDES	0.15	15	0.01		
ABCDE	0.03	1	0.03	3.61	0.0768
ABCDES	0.11	15	0.01		

Appendix VI: Target RT in Experiment 2

FACTORS

A) Cue Validity	1) Cued	2) Uncued	
B) ISI	1) Short	2) Long	
C) Congruency	1) Congruent	2) Incongruent	
D) Visual Field	1) Right	2) Left	
E) Orientation	1) Horizontal	2) Vertical	

* p < .05

ANALYSIS OF VARIANCE TABLE

SOURCE	SS	DF	MS	F	p
A	17649.55	1	17649.55	12.37	0.0031*
AS	21404.79	15	1426.99		
B	13393.99	1	13393.99	6.49	0.0223*
BS	30945.04	15	2063.00		
AB	14531.43	1	14531.43	19.68	0.0005*
ABS	11078.38	15	738.56		
C	4658.48	1	4658.48	10.97	0.0047*
CS	6368.99	15	424.60		
AC	639.77	1	639.77	1.99	0.1791
ACS	4831.86	15	322.12		
BC	416.40	1	416.40	1.49	0.2407
BCS	4185.83	15	279.06		
ABC	791.55	1	791.55	2.70	0.1214
ABCS	4405.36	15	293.69		
D	6972.97	1	6972.97	3.93	0.0660
DS	26611.35	15	1774.09		
AD	137.70	1	137.70	0.27	0.6101
ADS	7615.11	15	507.67		
BD	1373.58	1	1373.58	2.90	0.1092
BDS	7105.07	15	473.67		
ABD	448.67	1	448.67	1.23	0.2846
ABDS	5466.09	15	364.41		
CD	58.91	1	58.91	0.44	0.5189
CDS	2025.23	15	135.02		
ACD	1010.08	1	1010.08	4.51	0.0508
ACDS	3359.90	15	223.99		

```
BCD       223.41  1   223.41   0.66  0.4306
BCDS      5107.74  15   340.52

ABCD       646.65  1   646.65   1.37  0.2603
ABCDS      7088.16  15   472.54

E        1243.86  1  1243.86   0.18  0.6800
ES      105470.57  15  7031.37

AE         0.09  1    0.09   0.00# 0.9873
AES       5105.96  15   340.40

BE        94.23  1   94.23   0.99  0.3361
BES       1431.10  15   95.41

ABE        18.45  1   18.45   0.03  0.8554
ABES      8052.85  15   536.86

CE        31.89  1   31.89   0.09  0.7720
CES       5495.34  15   366.36

ACE       101.90  1   101.90   0.37  0.5514
ACES      4116.43  15   274.43

BCE       294.84  1   294.84   0.90  0.3579
BCES      4915.09  15   327.67

ABCE       213.19  1   213.19   0.63  0.4406
ABCES      5096.56  15   339.77

DE       13471.47  1  13471.47   1.95  0.1831
DES      103705.83  15  6913.72

ADE       7688.92  1  7688.92   3.56  0.0786
ADES      32363.38  15  2157.56

BDE        56.07  1   56.07   0.11  0.7486
BDES      7893.65  15   526.24

ABDE      3369.42  1  3369.42   2.30  0.1499
ABDES     21941.98  15  1462.80

CDE       300.11  1   300.11   0.60  0.4494
CDES      7461.70  15   497.45

ACDE      6305.85  1  6305.85  21.50  0.0003*
ACDES      4399.06  15   293.27

BCDE       443.03  1   443.03   1.28  0.2761
BCDES      5202.34  15   346.82

ABCDE      5194.10  1  5194.10  12.53  0.0030*
ABCDES     6220.46  15   414.70
```

Appendix VII: P1 Maximum Amplitude in Experiment 2 (75-115ms)

FACTORS

```
 A) Cuedness        1) Cued     2) Uncued
 B) ISI             1) Short    2) Long
 C) Congruency      1) Cong     2) Incong
 D) Visual Field    1) Right    2) Left
 E) Electrode       1) Lateral  2) Medial

   * p < .05

            ANALYSIS OF VARIANCE TABLE

SOURCE      SS   DF   MS    F    p
-------------------------------------------------------------
A         14.64  1   14.64  12.30  0.0032*
AS        17.86  15    1.19

B         50.37  1   50.37   4.84  0.0440*
BS        156.22  15   10.41

AB        10.55  1   10.55  13.83  0.0021*
ABS        11.45  15    0.76

C         6.07  1    6.07   6.34  0.0237*
CS        14.35  15    0.96

AC         0.07  1    0.07   0.34  0.5696
ACS        3.03  15    0.20

BC         5.95  1    5.95   7.36  0.0160*
BCS        12.13  15    0.81

ABC        0.51  1    0.51   1.72  0.2089
ABCS        4.42  15    0.29

D         20.96  1   20.96   8.60  0.0103*
DS        36.58  15    2.44

AD         0.00  1    0.00   0.00# 0.9635
ADS        2.74  15    0.18

BD         3.57  1    3.57   1.35  0.2640
BDS        39.79  15    2.65

ABD        0.08  1    0.08   0.15  0.7070
ABDS        7.80  15    0.52

CD         0.63  1    0.63   1.00  0.3328
CDS        9.51  15    0.63

ACD        0.03  1    0.03   0.10  0.7544
```

ACDS	3.72	15	0.25		
BCD	4.41	1	4.41	13.52	0.0022*
BCDS	4.89	15	0.33		
ABCD	0.03	1	0.03	0.09	0.7645
ABCDS	4.96	15	0.33		
E	0.17	1	0.17	0.08	0.7753
ES	29.81	15	1.99		
AE	0.02	1	0.02	0.07	0.7903
AES	3.62	15	0.24		
BE	2.31	1	2.31	1.60	0.2256
BES	21.69	15	1.45		
ABE	0.05	1	0.05	0.50	0.4919
ABES	1.53	15	0.10		
CE	1.28	1	1.28	20.19	0.0004*
CES	0.95	15	0.06		
ACE	0.00	1	0.00	0.02	0.9037
ACES	0.50	15	0.03		
BCE	0.93	1	0.93	10.41	0.0056*
BCES	1.34	15	0.09		
ABCE	0.01	1	0.01	0.19	0.6687
ABCES	0.92	15	0.06		
DE	1.22	1	1.22	1.35	0.2632
DES	13.56	15	0.90		
ADE	0.04	1	0.04	1.14	0.3033
ADES	0.47	15	0.03		
BDE	1.06	1	1.06	4.16	0.0593
BDES	3.80	15	0.25		
ABDE	0.09	1	0.09	2.13	0.1648
ABDES	0.65	15	0.04		
CDE	0.01	1	0.01	0.16	0.6990
CDES	1.04	15	0.07		
ACDE	0.03	1	0.03	0.70	0.4145
ACDES	0.61	15	0.04		
BCDE	0.00	1	0.00	0.01	0.9207
BCDES	0.74	15	0.05		
ABCDE	0.00	1	0.00	0.01	0.9151
ABCDES	0.60	15	0.04		

Appendix VIII: IIN Maximum Amplitude in Experiment 2 (200-300ms)

FACTORS

A) Cuedness	1) Cued	2) Uncued
B) ISI	1) Short	2) Long
C) Congruency	1) Cong	2) Incong
D) Electrode	1) Medial	2) Lateral

* p < .05

ANALYSIS OF VARIANCE TABLE

SOURCE	SS	DF	MS	F	p
A	3.52	1	3.52	8.17	0.0119*
AS	6.45	15	0.43		
B	7.29	1	7.29	3.33	0.0881
BS	32.86	15	2.19		
AB	10.18	1	10.18	22.53	0.0003*
ABS	6.77	15	0.45		
C	0.02	1	0.02	0.23	0.6410
CS	1.47	15	0.10		
AC	0.02	1	0.02	0.18	0.6805
ACS	1.30	15	0.09		
BC	0.95	1	0.95	5.22	0.0374*
BCS	2.74	15	0.18		
ABC	0.64	1	0.64	7.41	0.0158*
ABCS	1.30	15	0.09		
D	79.92	1	79.92	130.43	0.0000*
DS	9.19	15	0.61		
AD	0.19	1	0.19	3.03	0.1021
ADS	0.94	15	0.06		
BD	2.36	1	2.36	18.35	0.0007*
BDS	1.93	15	0.13		
ABD	0.50	1	0.50	14.87	0.0016*
ABDS	0.50	15	0.03		
CD	0.04	1	0.04	1.50	0.2400
CDS	0.43	15	0.03		
ACD	0.00	1	0.00	0.28	0.6069
ACDS	0.20	15	0.01		
BCD	0.19	1	0.19	9.53	0.0075*

BCDS	0.31	15	0.02
ABCD	0.05	1	0.05
ABCDS	0.33	15	0.02

Appendix IX: P2 Maximum Amplitude in Experiment 2 (180-250ms)

FACTORS

```
 A) Cue Validity    1) Cued             2) Uncued
 B) ISI             1) Short            2) Long
 C) Congruency      1) Cong             2) Incong
 D) Electrode       1) Central Anterior 2) Central
```

* p < .05

ANALYSIS OF VARIANCE TABLE

SOURCE	SS	DF	MS	F	p
MEAN	2539.34	1	2539.34	190.49	0.0000*
S	199.96	15	13.33		
A	7.11	1	7.11	3.92	0.0663
AS	27.19	15	1.81		
B	121.40	1	121.40	28.75	0.0001*
BS	63.33	15	4.22		
AB	0.03	1	0.03	0.04	0.8389
ABS	10.20	15	0.68		
C	0.37	1	0.37	0.58	0.4578
CS	9.47	15	0.63		
AC	3.09	1	3.09	3.95	0.0654
ACS	11.73	15	0.78		
BC	2.07	1	2.07	1.75	0.2055
BCS	17.74	15	1.18		
ABC	3.21	1	3.21	8.37	0.0112*
ABCS	5.75	15	0.38		
D	10.48	1	10.48	11.11	0.0045*
DS	14.15	15	0.94		
AD	0.05	1	0.05	1.27	0.2772
ADS	0.64	15	0.04		
BD	0.04	1	0.04	0.12	0.7371
BDS	4.85	15	0.32		
ABD	0.01	1	0.01	0.29	0.5992
ABDS	0.28	15	0.02		
CD	0.19	1	0.19	2.98	0.1047
CDS	0.94	15	0.06		
ACD	0.00	1	0.00	0.16	0.6918

ACDS	0.28	15	0.02		
BCD	0.08	1	0.08	6.38	0.0233*
BCDS	0.18	15	0.01		
ABCD	0.08	1	0.08	2.12	0.1656
ABCDS	0.53	15	0.04		

Appendix X: P300 Maximum Amplitude in Experiment 2 (300-500ms)

FACTORS

```
 A) Cuedness        1) Cued            2) Uncued
 B) ISI             1) Short           2) Long
 C) Congruency      1) Cong            2) Incong
 D) Visual Field    1) Right           2) Left
 E) Electrode       1) Midline Center  2) Central Posterior
```

* p < .05

ANALYSIS OF VARIANCE TABLE

SOURCE	SS	DF	MS	F	p
A	31.00	1	31.00	36.19	0.0000*
AS	12.85	15	0.86		
B	52.54	1	52.54	32.92	0.0000*
BS	23.94	15	1.60		
AB	1.93	1	1.93	3.42	0.0842
ABS	8.46	15	0.56		
C	0.22	1	0.22	1.27	0.2780
CS	2.59	15	0.17		
AC	0.00	1	0.00	0.00#	0.9596
ACS	3.72	15	0.25		
BC	6.81	1	6.81	13.16	0.0025*
BCS	7.76	15	0.52		
ABC	0.63	1	0.63	3.66	0.0751
ABCS	2.60	15	0.17		
D	1.44	1	1.44	0.42	0.5290
DS	51.84	15	3.46		
AD	0.01	1	0.01	0.33	0.5767
ADS	0.32	15	0.02		
BD	1.47	1	1.47	20.22	0.0004*
BDS	1.09	15	0.07		
ABD	0.01	1	0.01	1.01	0.3308
ABDS	0.16	15	0.01		
CD	0.00	1	0.00	0.03	0.8606
CDS	0.78	15	0.05		
ACD	0.01	1	0.01	0.63	0.4413

ACDS	0.19	15	0.01		
BCD	0.03	1	0.03	1.51	0.2376
BCDS	0.26	15	0.02		
ABCD	0.10	1	0.10	4.87	0.0433*
ABCDS	0.30	15	0.02		

Magnocellular and Parvocellular Properties

Property	**M Stream**	**P Stream**
Spatial frequency sensitivity (SF)	Low SF	High SF
Ganglion population	Few	Many
Receptive field size	Large	Small
Luminance contrast gain	High	Low
Chromatic opponency	No	Yes
Motion sensitive	Yes	No
V1 projection	4Cα	4Cβ
Conduction velocity	Fast	Slow

Table 1: Response Characteristics of M and P cells

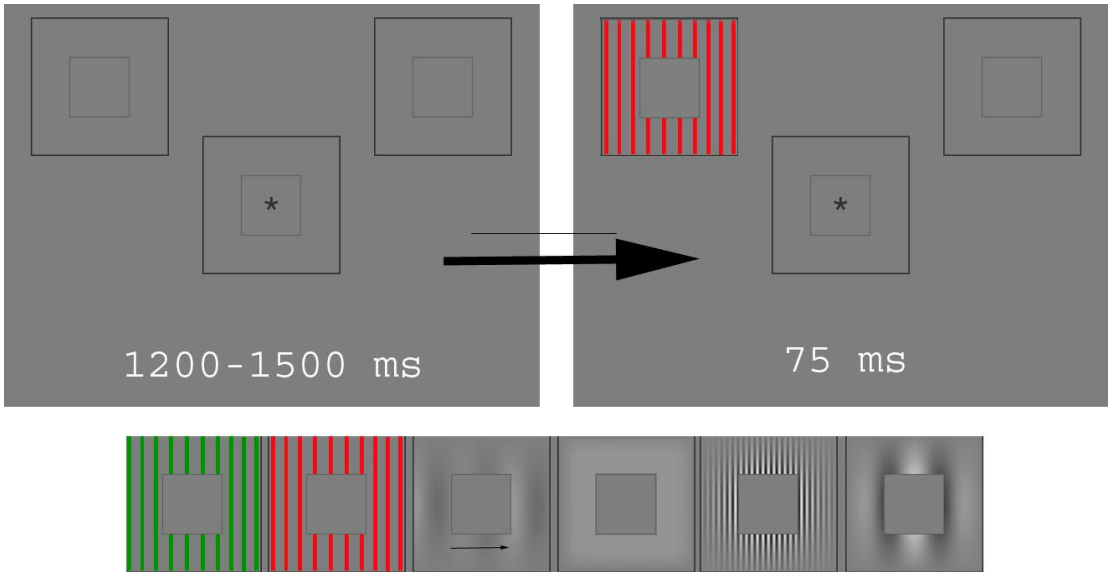


Figure 1: Above: Background image with stimulus placeholders used in pilot experiments 1 and 2. Below: Stimuli used in pilot studies 1 and 2. From left to right; high spatial frequency/green grating, high spatial frequency/red grating, low spatial frequency/motion, low spatial frequency/low luminance contrast, high spatial frequency/high contrast, low spatial frequency/high contrast.

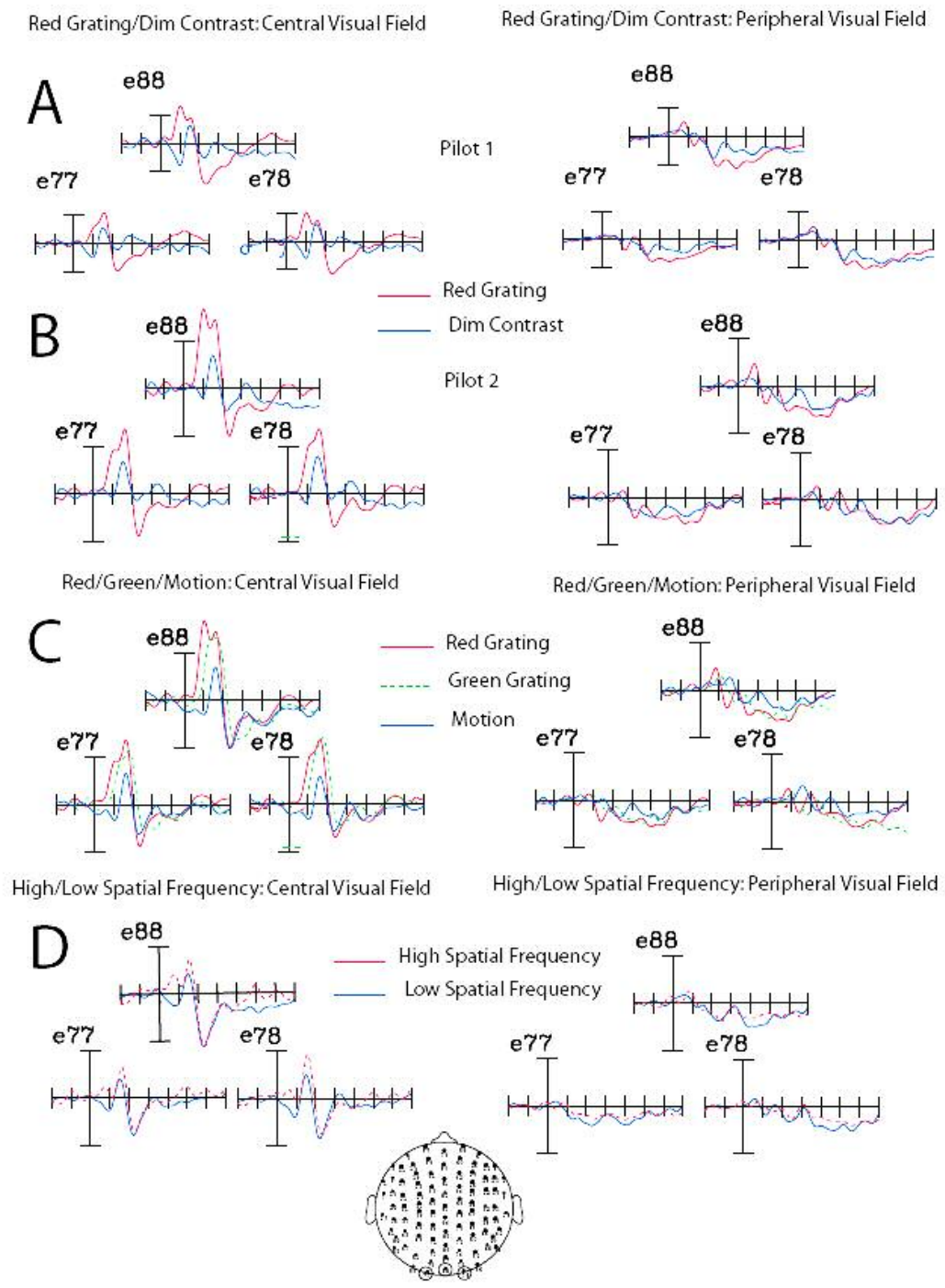


Figure 2: ERPs to stimuli in pilot studies 1 and 2. Note. Each tick mark represents 100ms and each plot is on a +/- 2 microvolt scale. Electrode location numbers are represented on the electrode map at the bottom of the figure. Electrode 88 corresponds to Oz in the 10/20 system; 77 and 78 correspond to O1 and O2 respectively. A) ERPs to the red grating and dim luminance contrast stimuli in the first pilot experiment. B) Pilot study 2. ERPs to the same stimuli used in the first pilot experiment. This second pilot experiment produced similar evoked responses at the same electrodes when compared to pilot study 1. C) Pilot study 2. ERPs to red grating, green grating and motion stimuli. D) Pilot study 2. ERPs to high and low spatial frequency stimuli at the same luminance contrast.

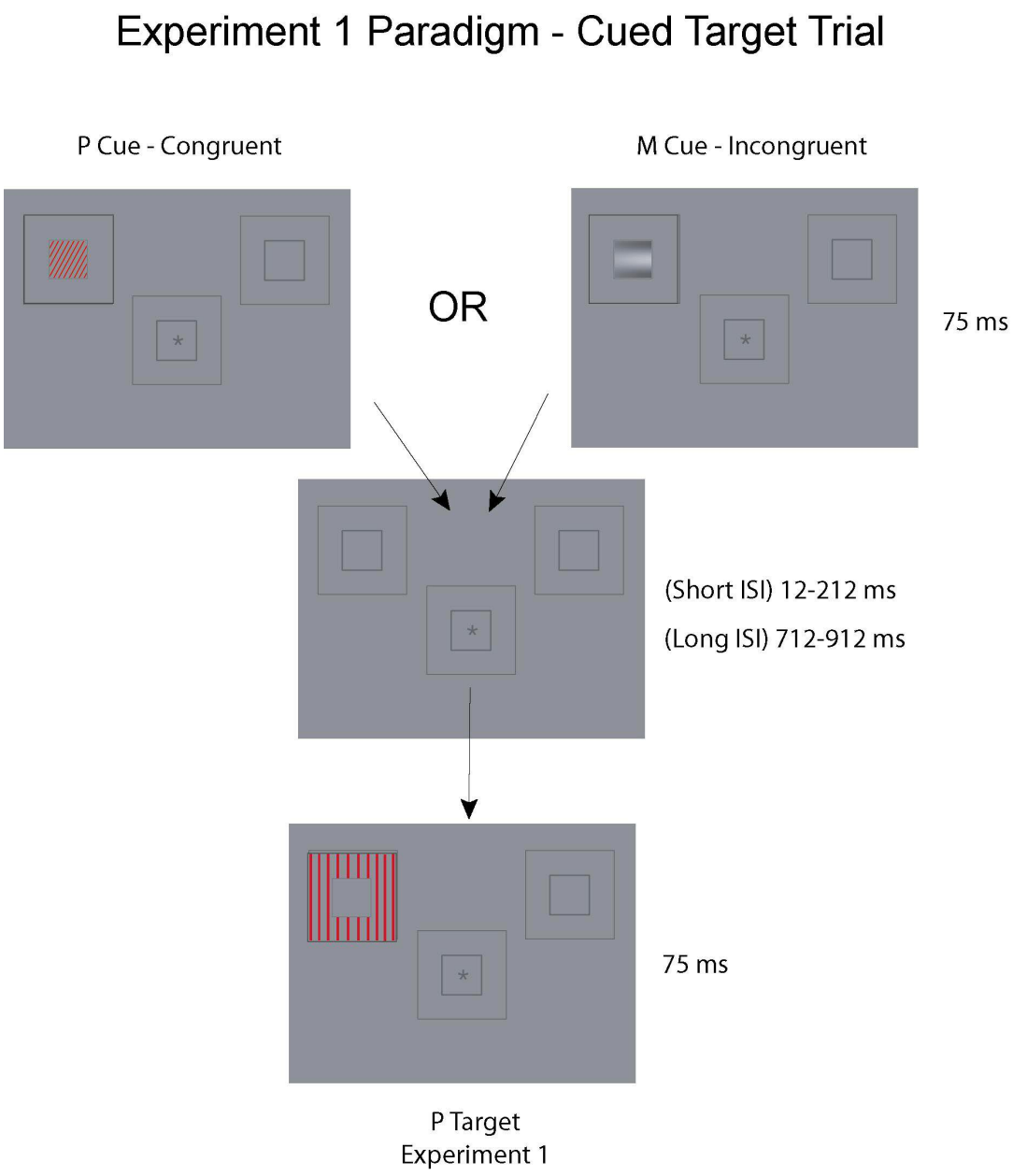
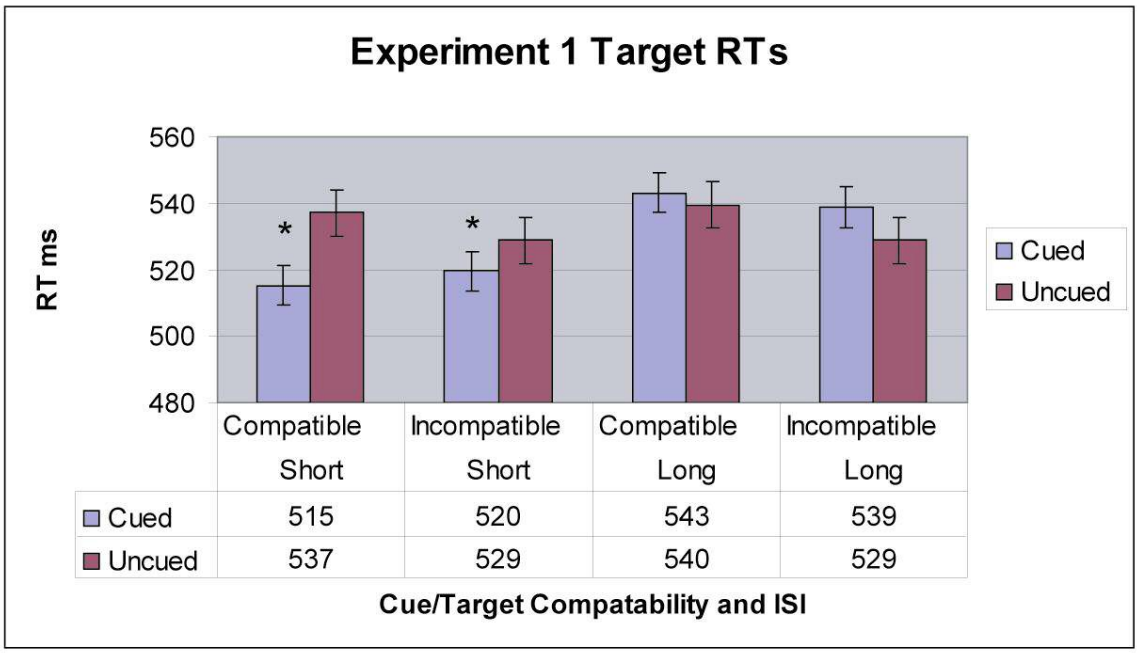
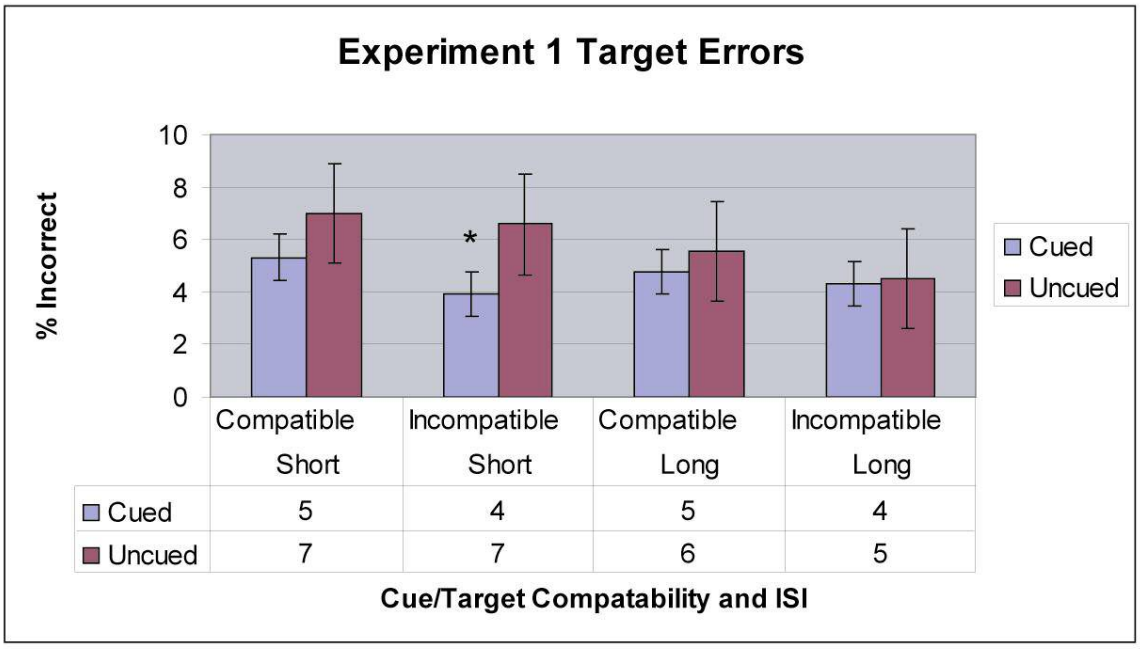


Figure 3: Cue/target paradigm used in Experiments 1.





* $p < .05$

Figure 4: Mean target RT (A) and errors (B) in Experiment 1. Error bars represent 1 standard error of the mean. Condition means are presented in the data table beneath each figure.

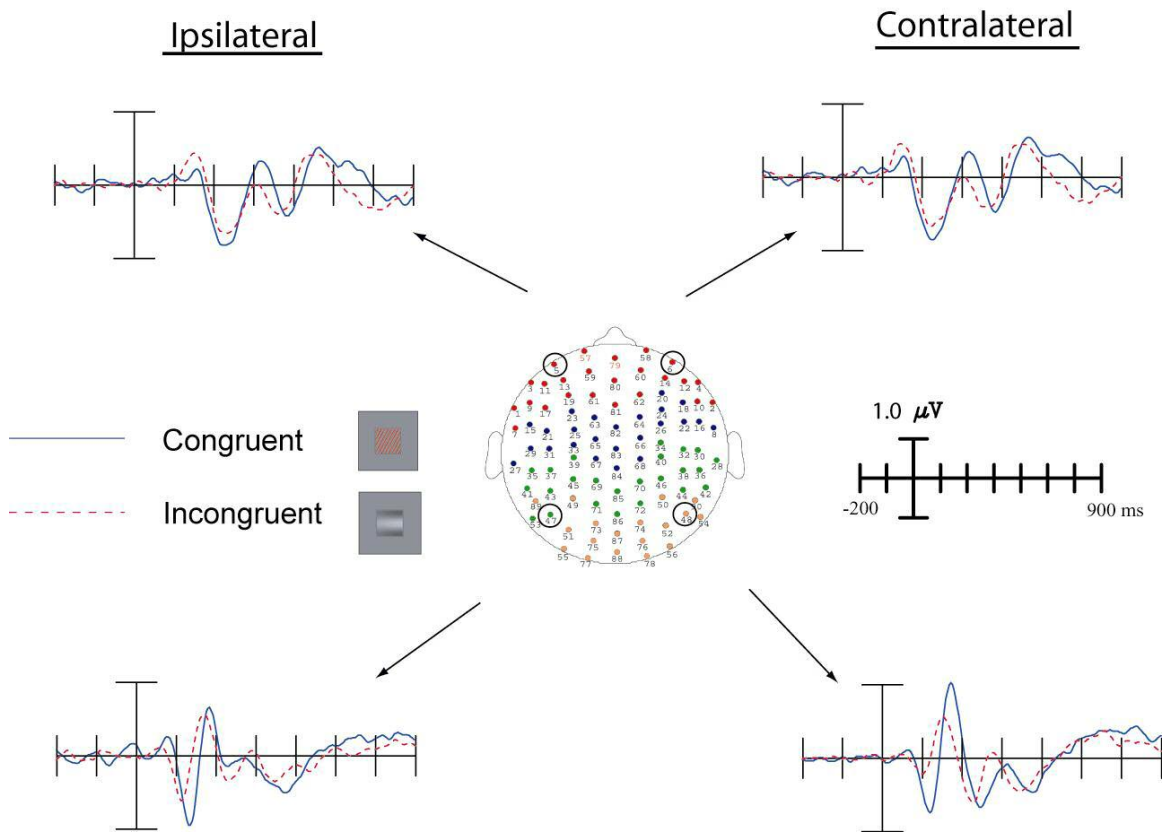


Figure 5: Cue evoked activity from Experiments 1. ERP waveforms were obtained from the locations outlined in the electrode montage presented in the center.

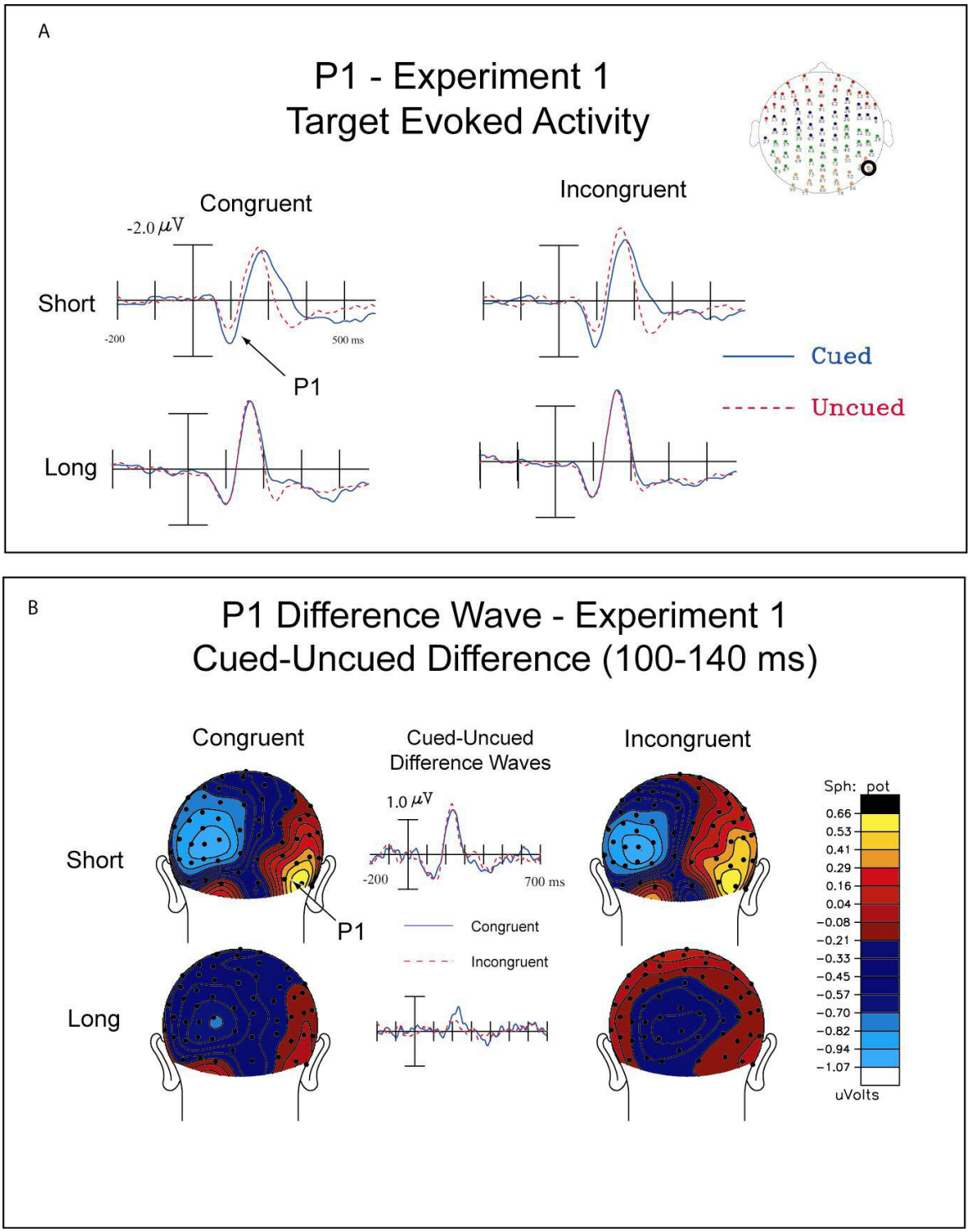


Figure 6: (A) Target evoked P1 component in Experiment 1 for cued and uncued trials. waveforms are presented from the circled electrode in the upper right. note that the right hemisphere represents contralateral activity while ipsilateral activity is represented over the left hemisphere (B) Cued-Uncued difference waves and topographic voltage maps of the cued-uncued difference.

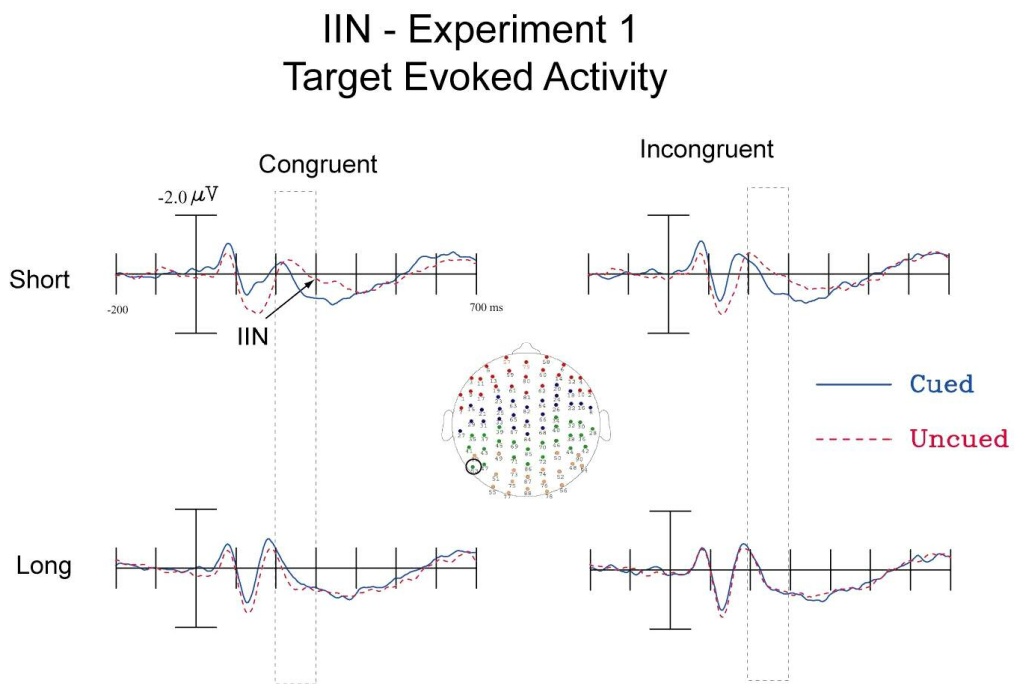


Figure 7: ERPs to target stimuli in Experiment 1 highlighting the IIN component. Statistical analysis was tested over a 200-300ms window indicated by the dashed rectangles.

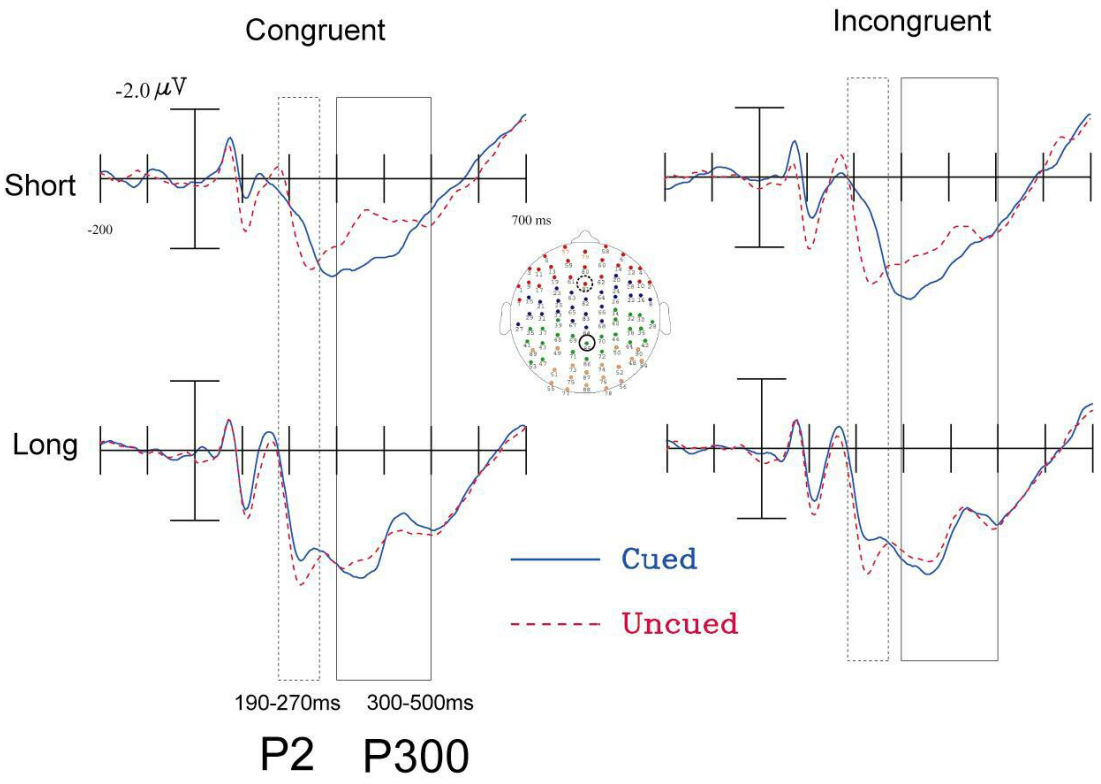


Figure 8: ERP target waveforms displaying the P2 and P300 components in Experiment 1. P2 activity was analyzed over anterior electrodes while the P300 was analyzed over central/posterior electrodes

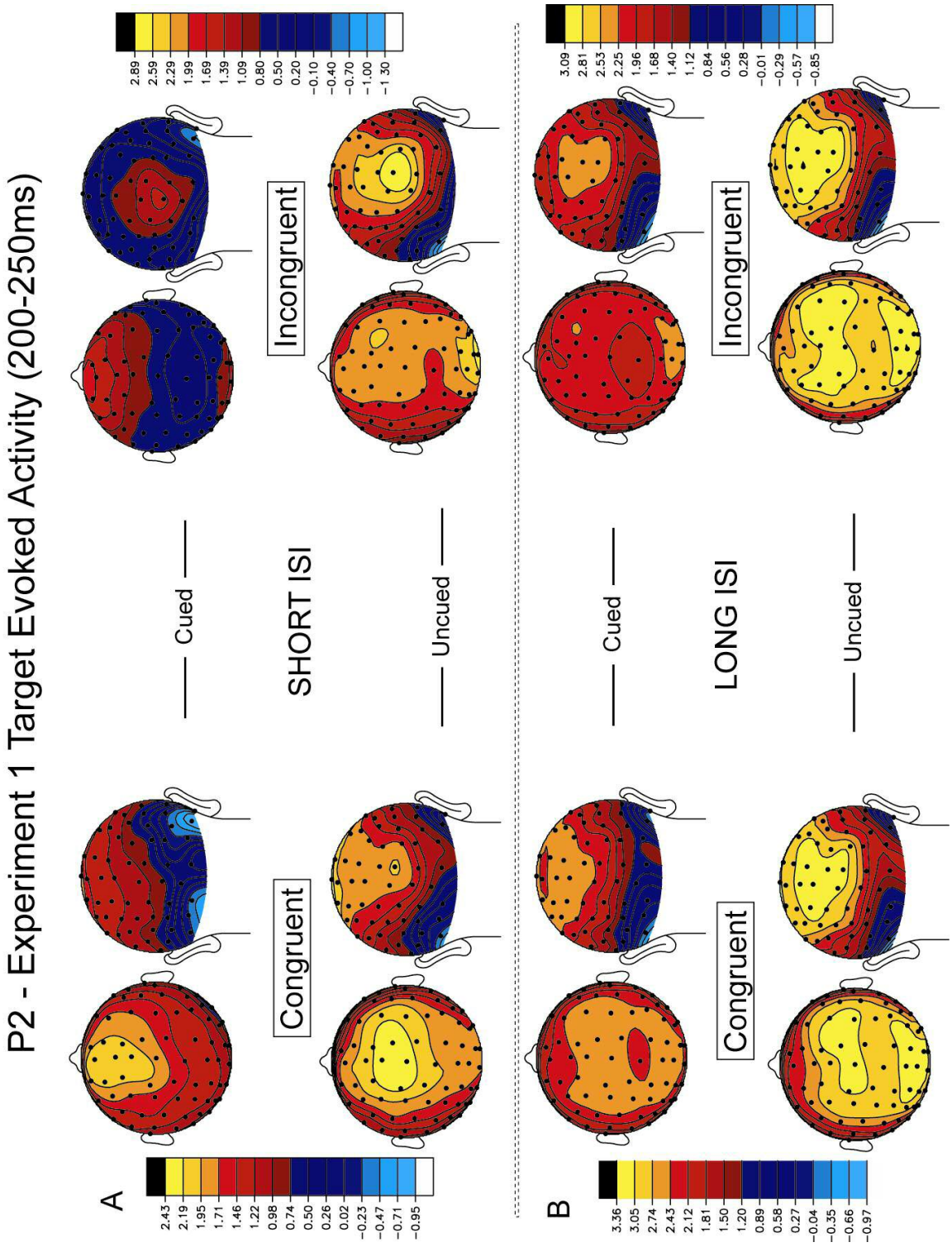


Figure 9: Topographic voltage maps to target stimuli in Experiment 1 highlighting the P2 component.

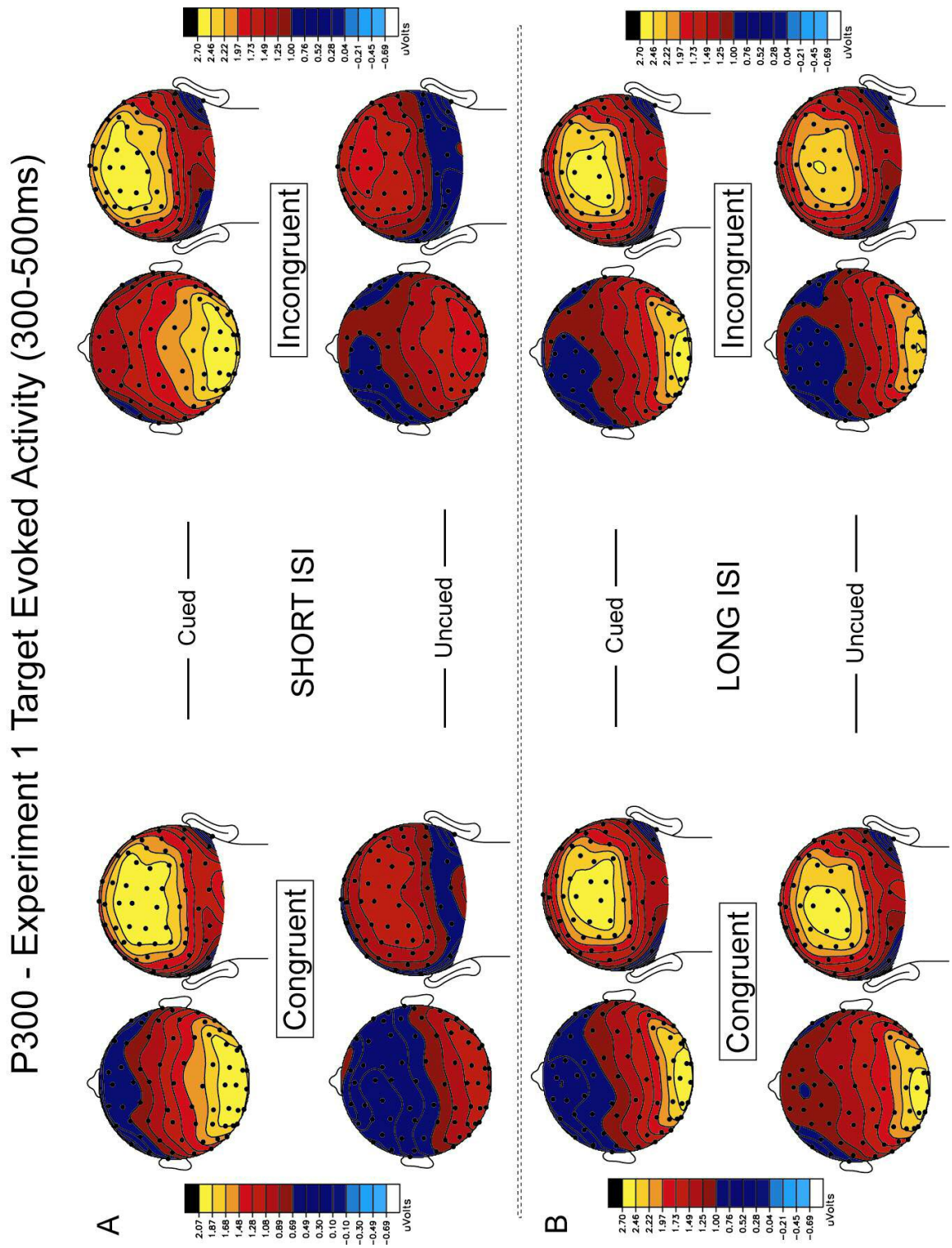


Figure 10: Topographic voltage maps of the P300 in Experiment 1.

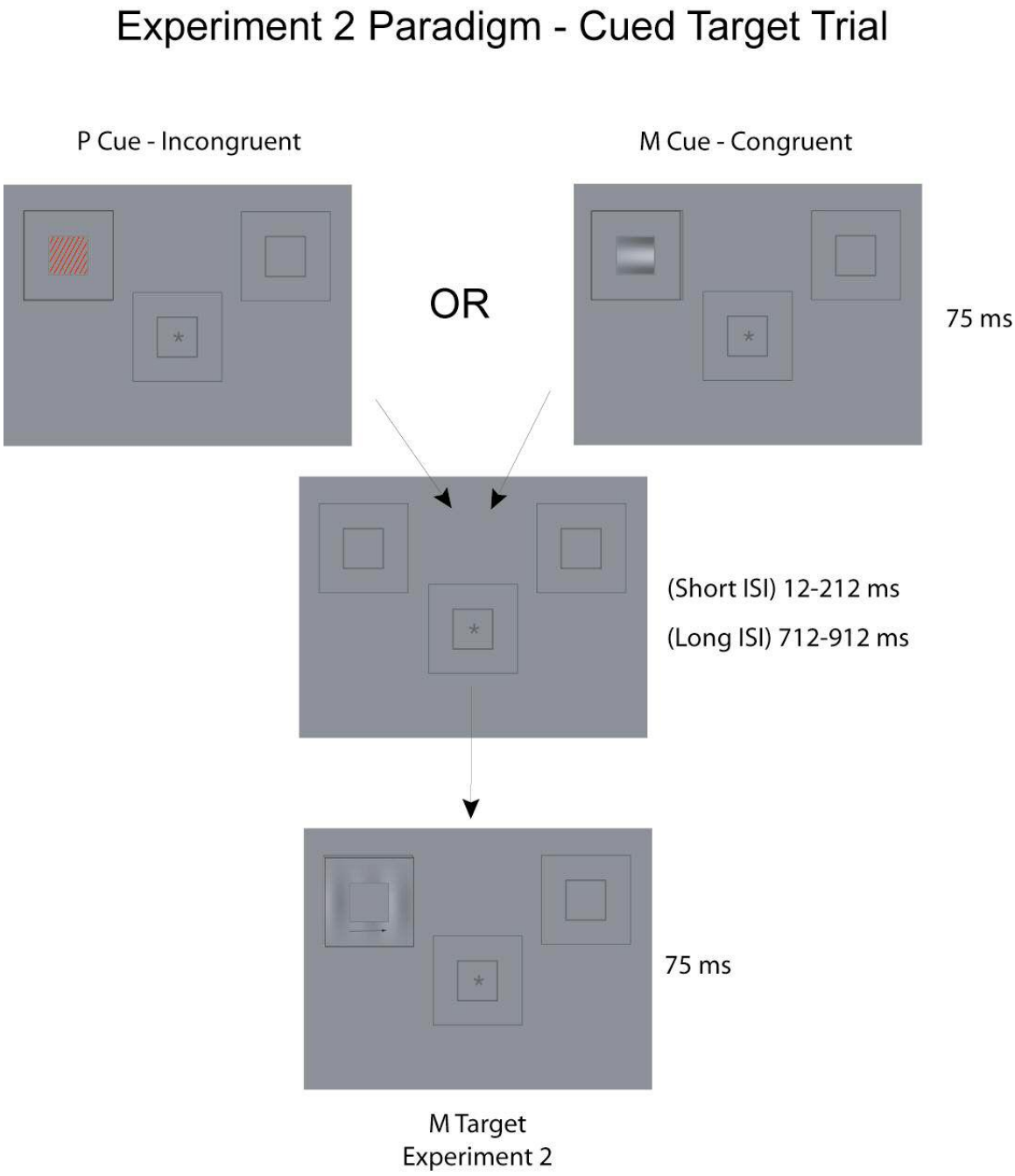
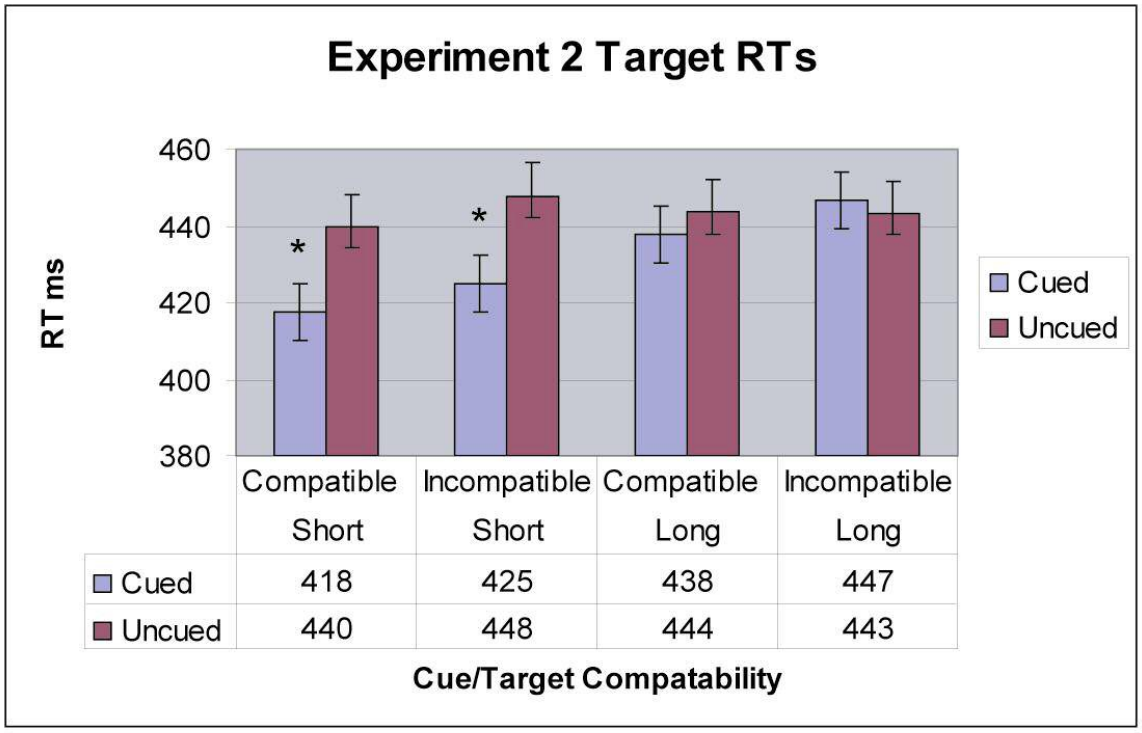
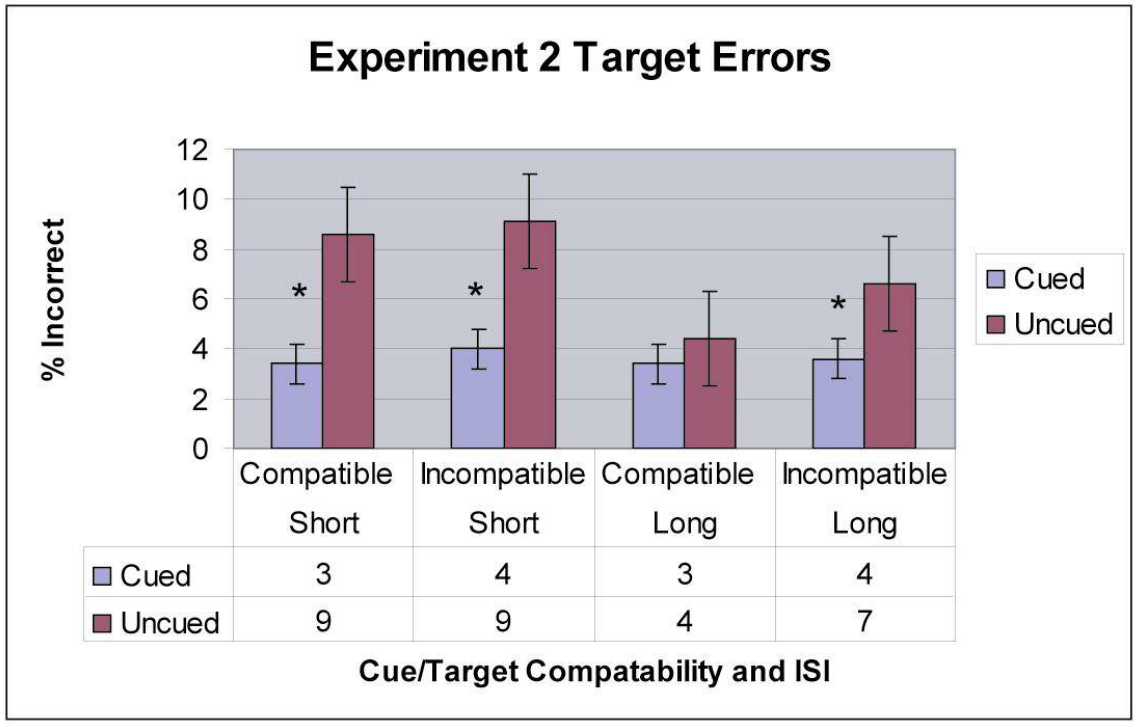


Figure 11: Cue target paradigm used in Experiment 2.





* $p < .05$

Figure 12: Mean target RT (A) and errors (B) in Experiment 2. Error bars represent 1 standard error of the mean. Condition means are presented in the data table beneath each figure.

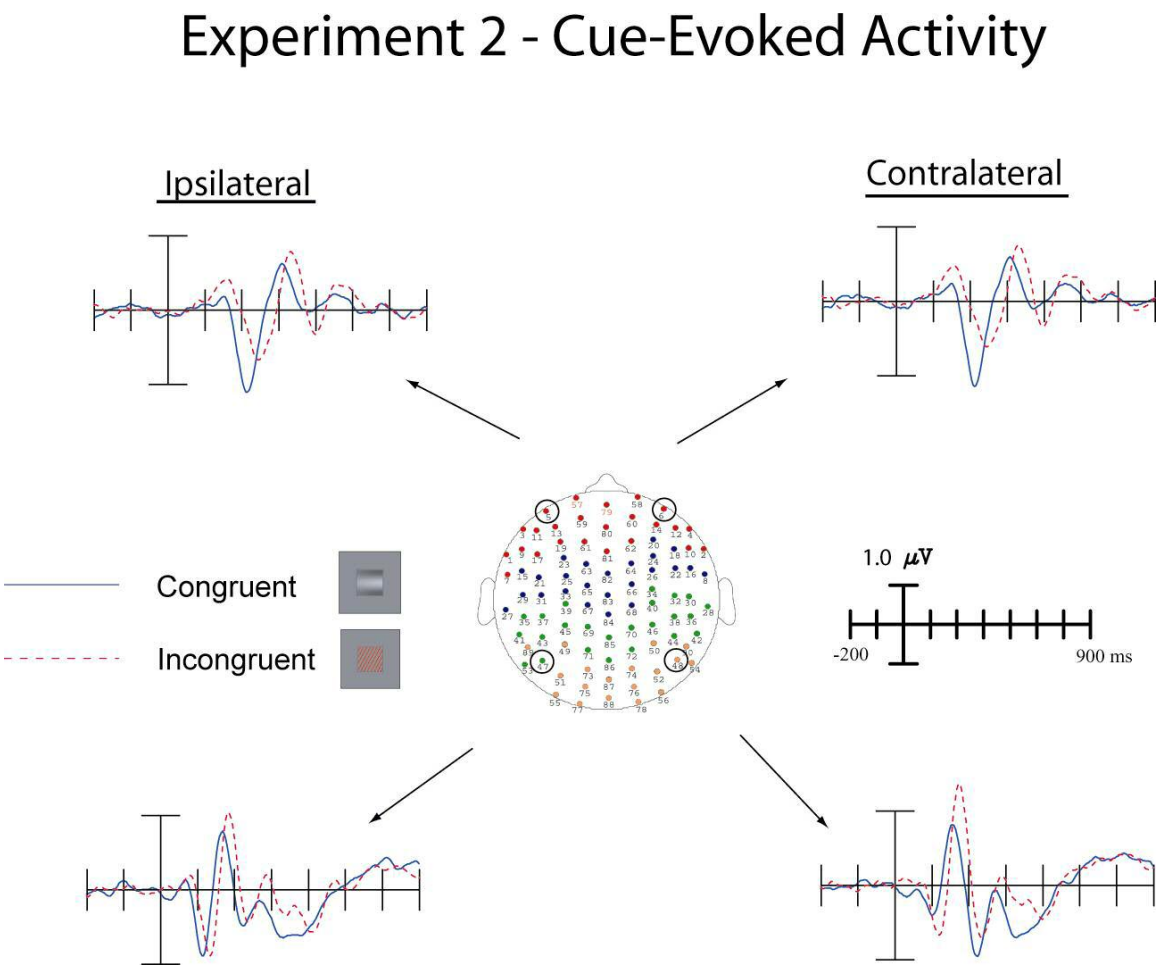


Figure 13: Cue-evoked activity in Experiment 2.

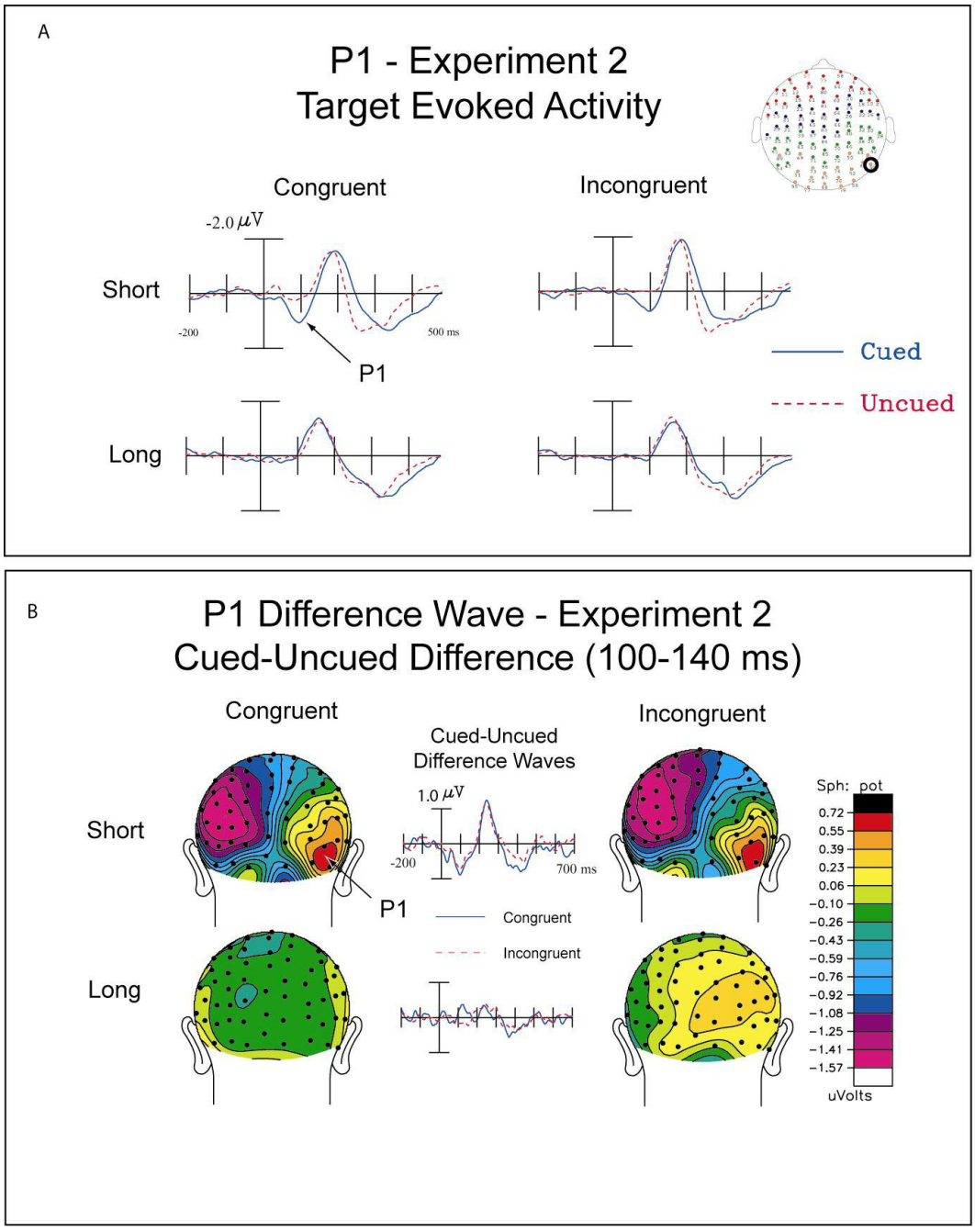


Figure 14: Above: Target evoked P1 component in Experiment 2 for cued and uncued trials. Below: Cued-Uncued difference waves and topographic voltage maps of the difference.

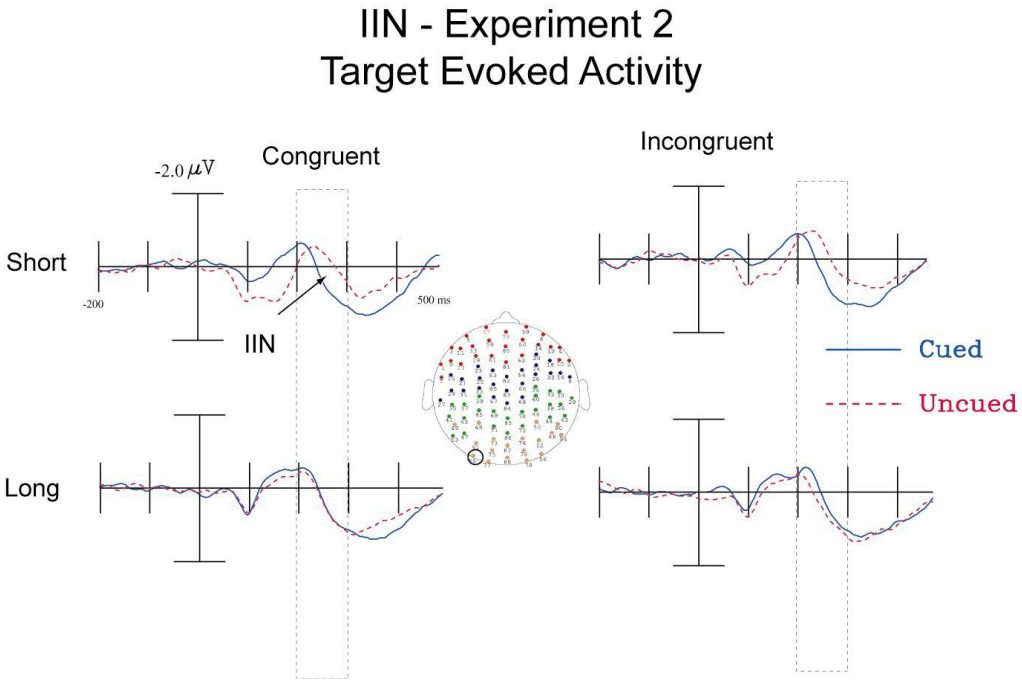


Figure 15: Target evoked activity over occipital electrodes ipsilateral to target visual field. ERPs to target stimuli in Experiment 2 highlighting the significant difference between cued and uncued trials for the IIN component only at the short ISI.

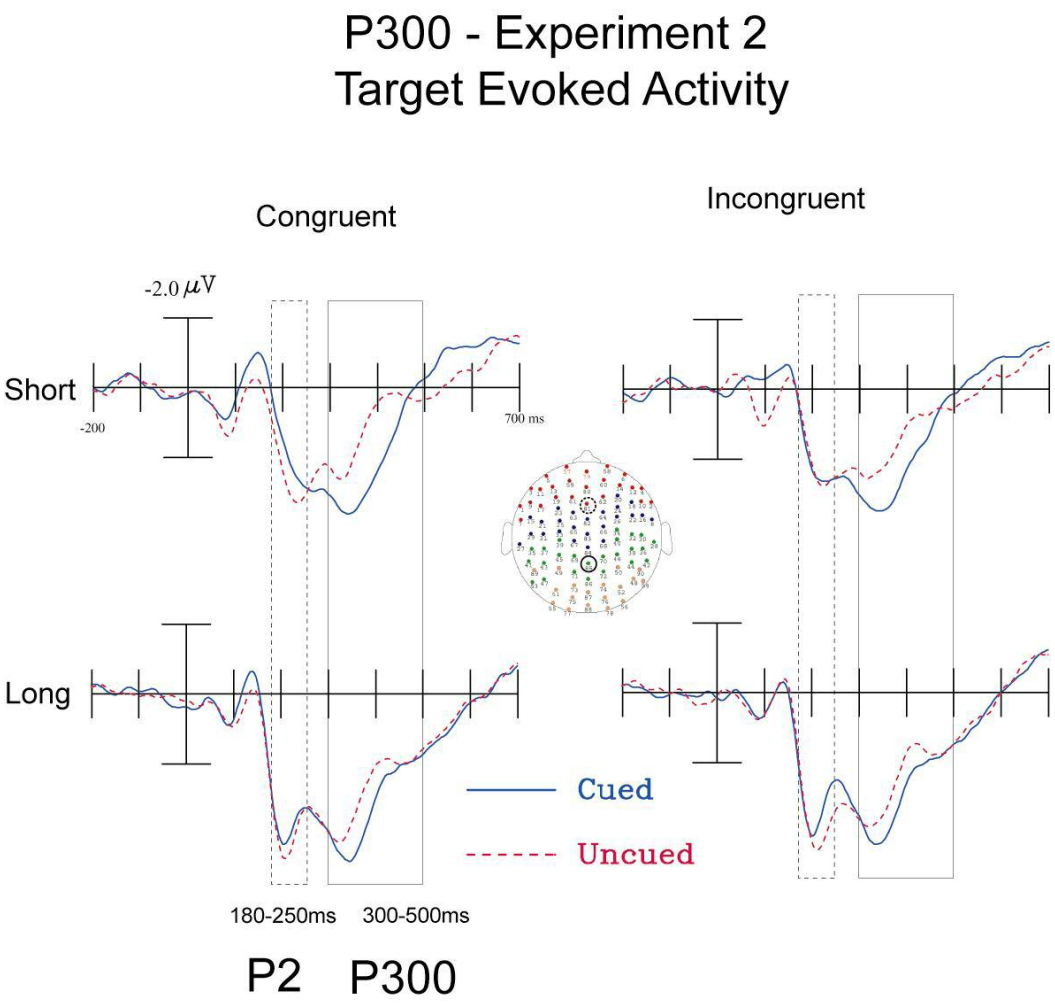


Figure 16: ERPs to target stimuli in Experiment 2 for the P2 and P300 components.

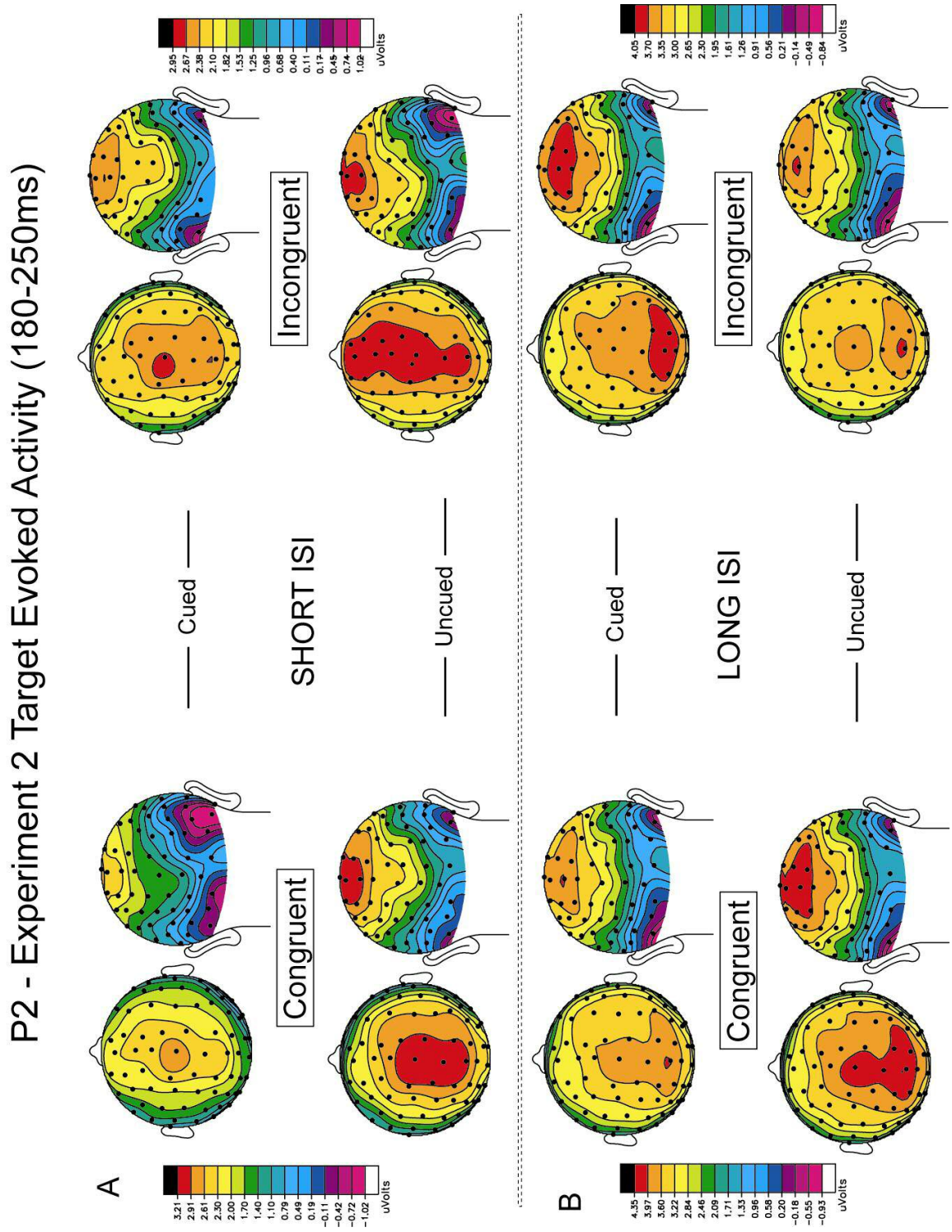


Figure 17: Topographic voltage maps to target stimuli in Experiment 2 highlighting the P2 component.

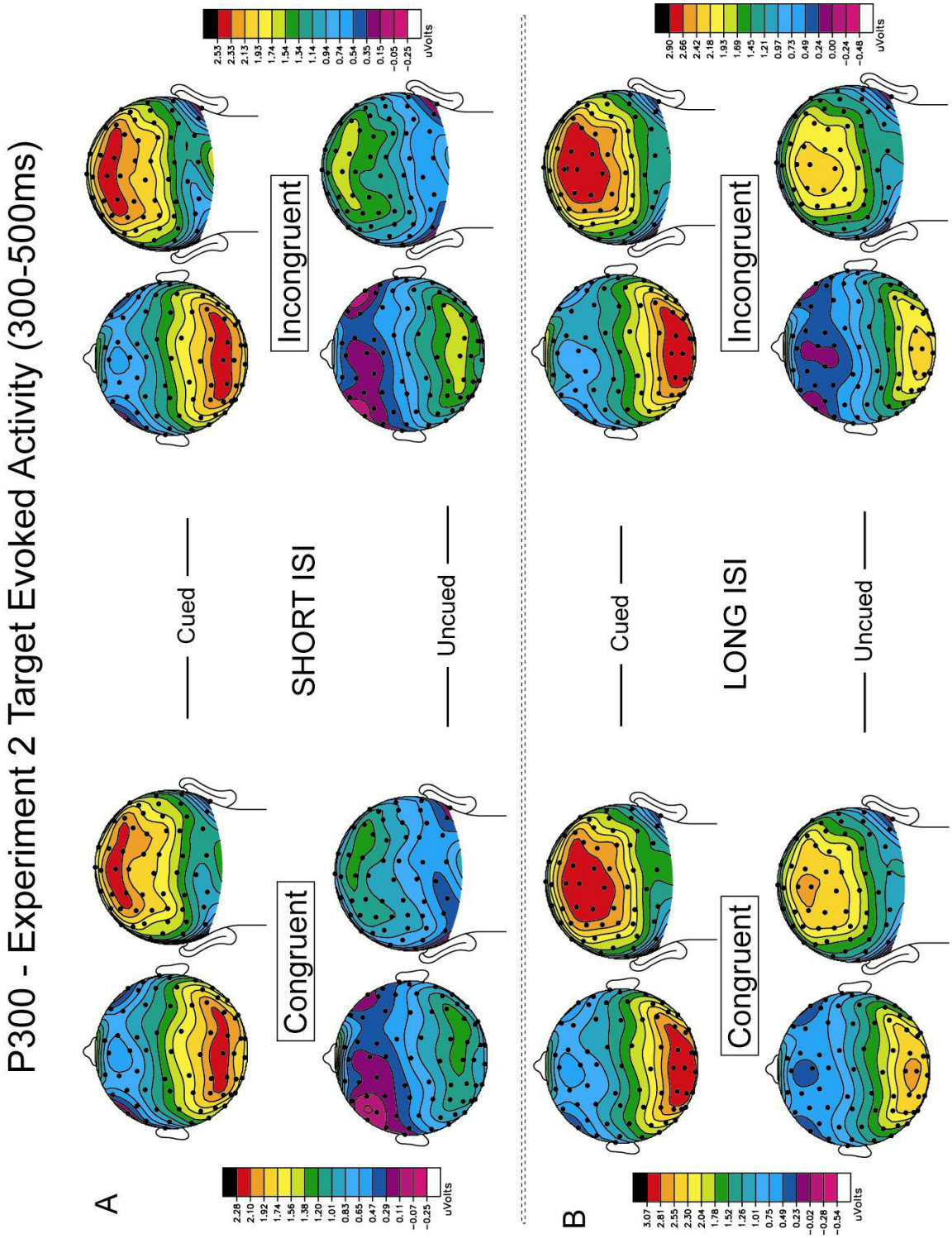


Figure 18: Topographic voltage maps to target stimuli in Experiment 2 highlighting the P2 component.

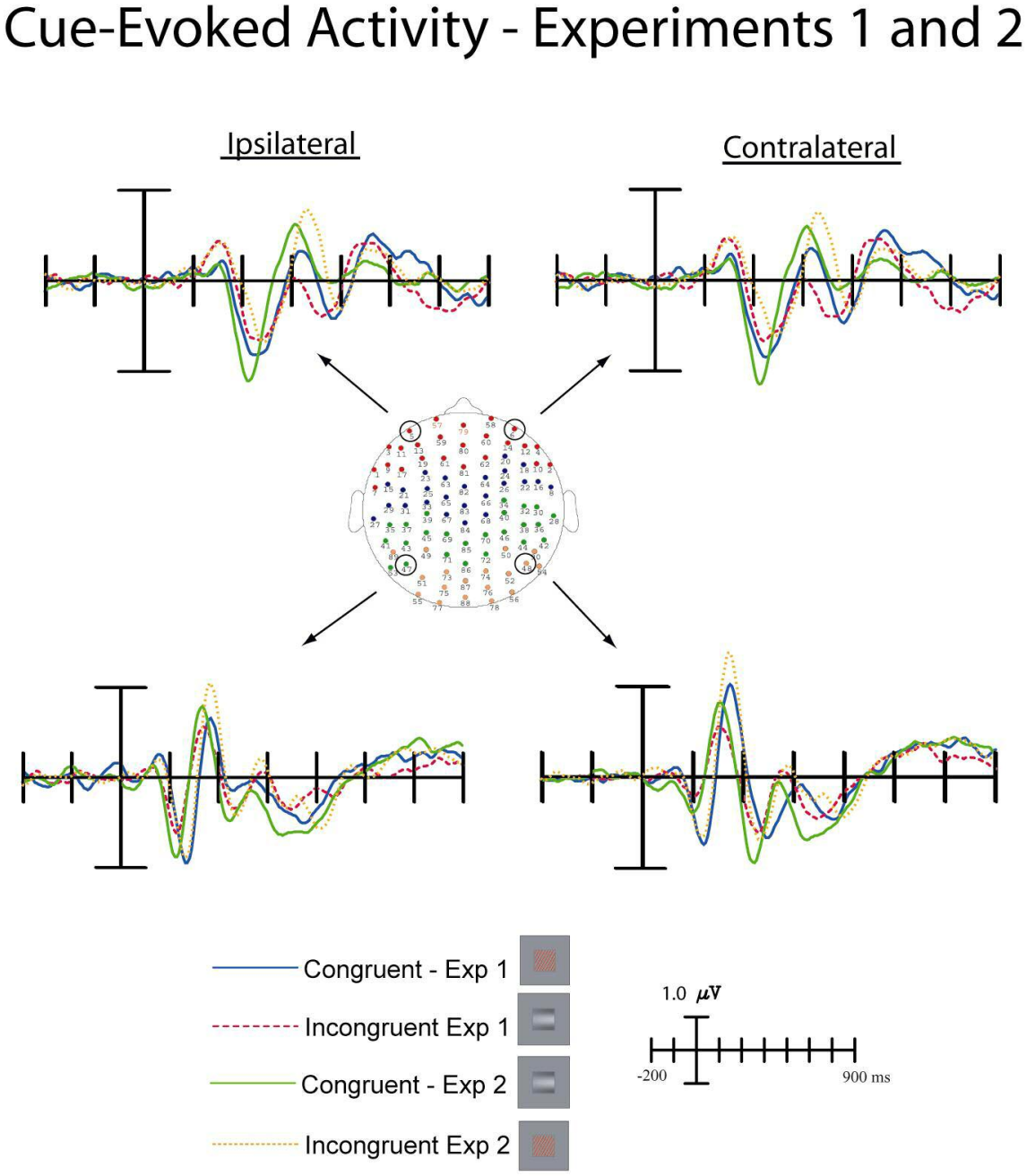


Figure 19: ERPs to cue stimuli in Experiments 1 and 2.

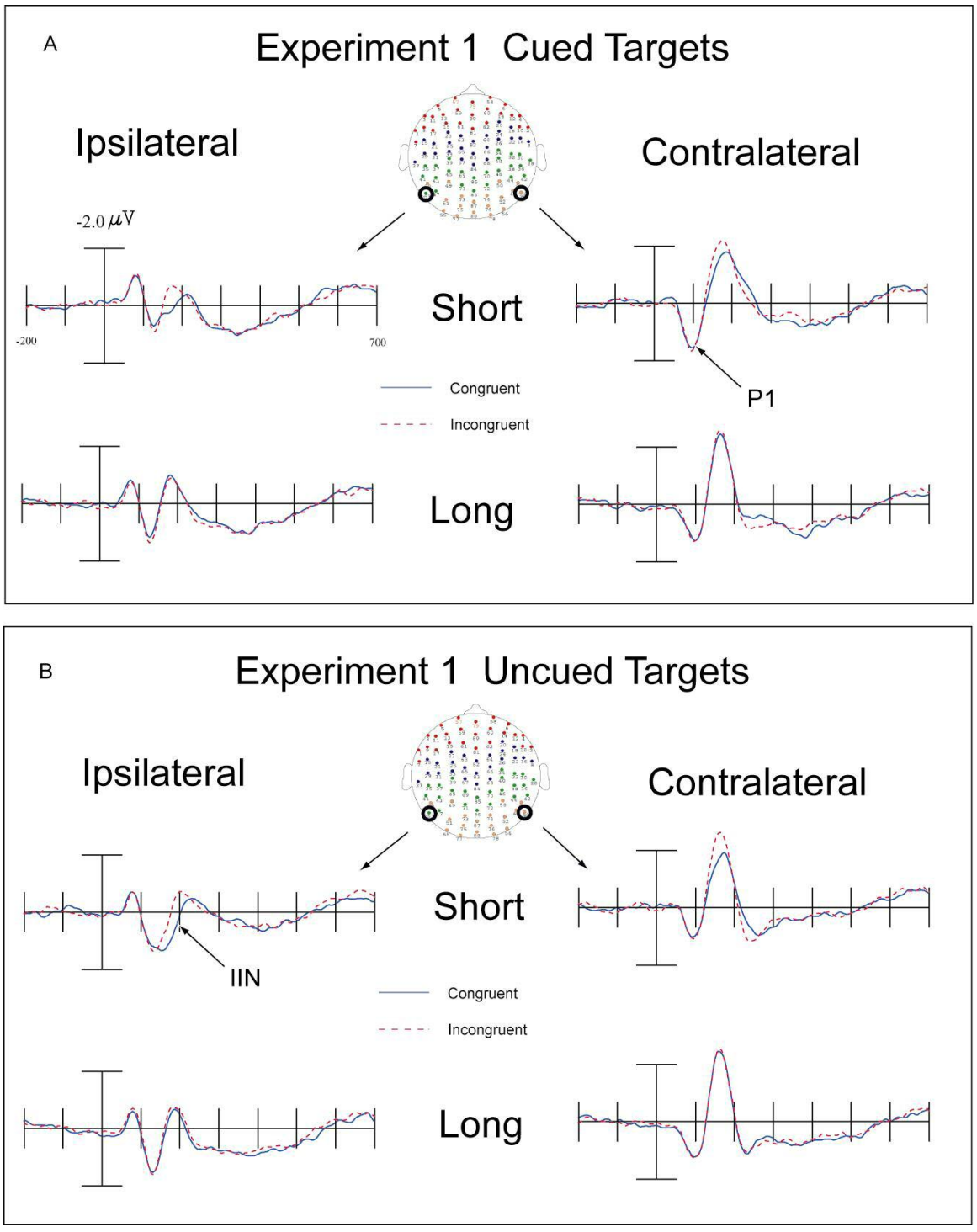


Figure 20: A. Cued ERPs in Experiment 1. B. Uncued ERPs in Experiment 1. ERPs were obtained from the electrode locations denoted in the electrode montage located in the center of each figure.

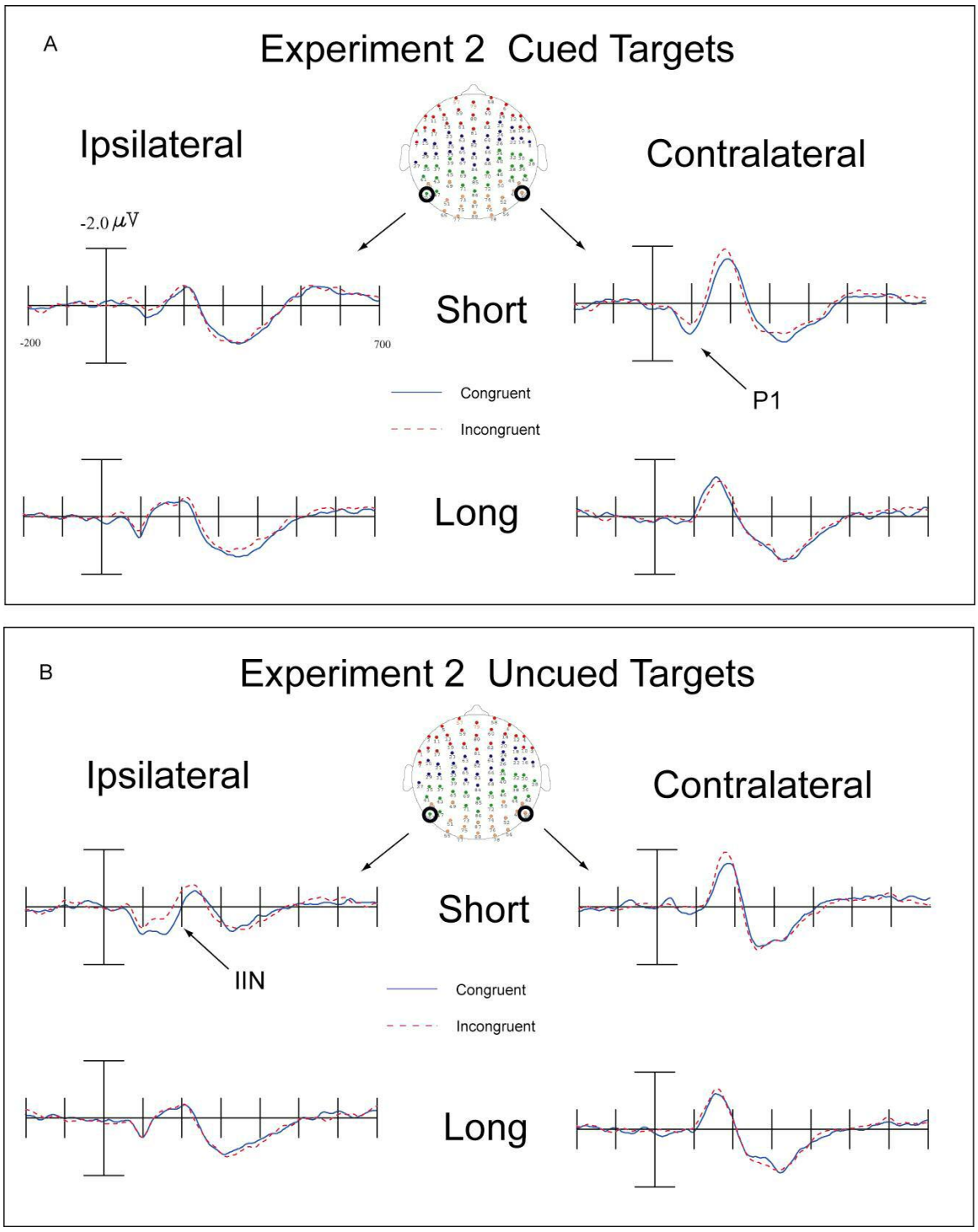
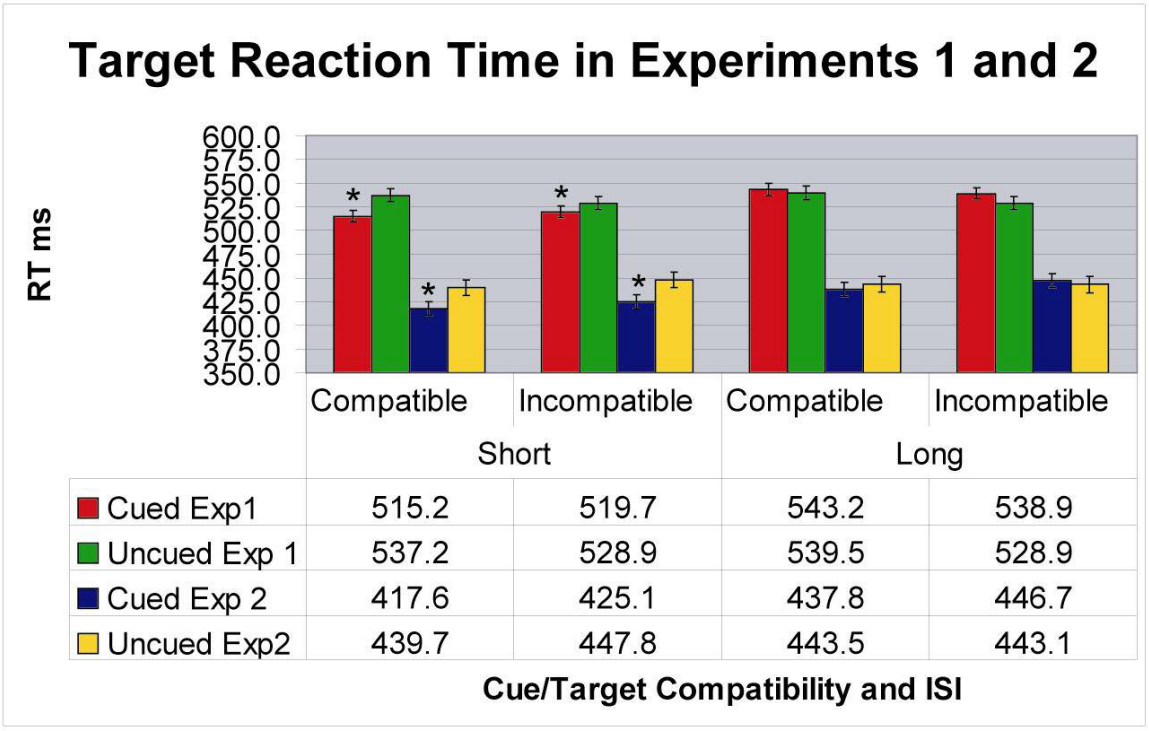


Figure 21: A. Cued ERPs in Experiment 2. B. Uncued ERPs in Experiment 1. ERPs were obtained from the electrode locations denoted in the electrode montage located in the center of each figure.



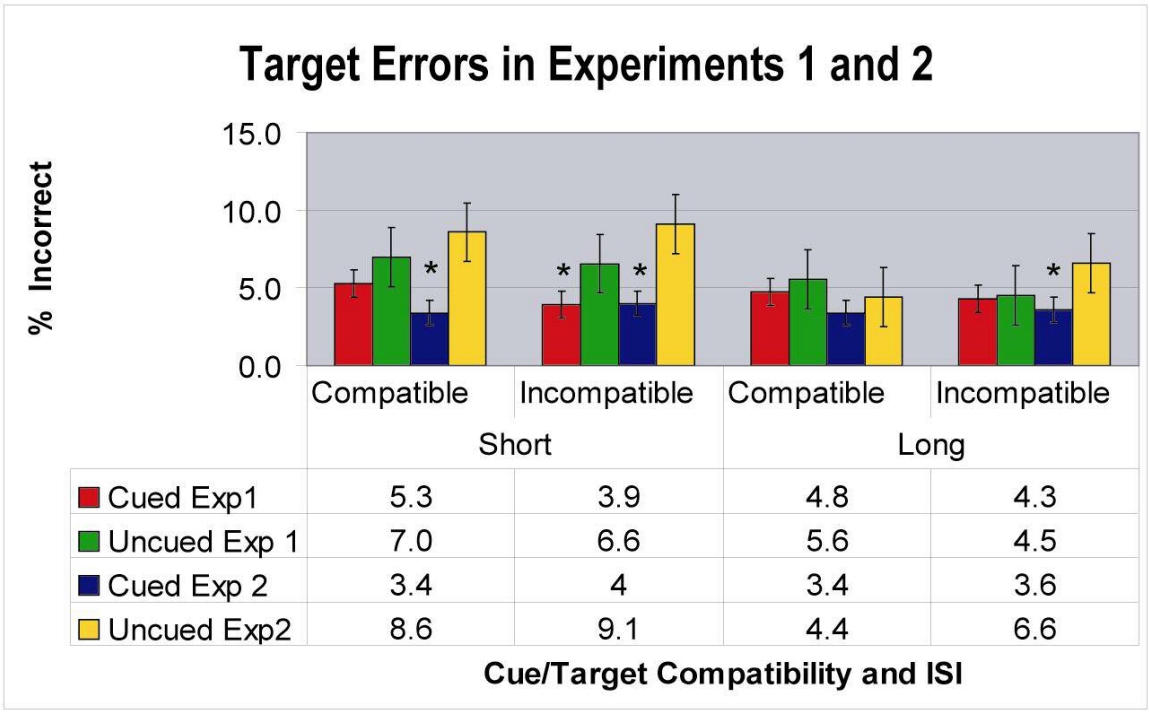


Figure 22: Target RTs and errors in Experiment 1 and 2.

References

Anderson, S.J., Mullen, K.T., and Hess, R.F. (1991). Human peripheral spatial resolution for achromatic and chromatic stimuli: limits imposed by optical and retinal factors. *Journal of Physiology, 442*, 47-64.

Anllo-Vento, L., and Hillyard, SA. (1996). Selective attention to the color and direction of moving stimuli: electrophysiological correlates of hierarchical feature selection, *Perception and Psychophysics, 58*, 191-206.

Ansorage, U. and Heumann, M. Top-down contingencies in peripheral cueing: The roles of color and location. *Journal of Experimental Psychology: Human Perception and Performance, 29*, 937-948.

Arnott, SR., Pratt, J., Shore, DI. & Alain, C. (2001). Attentional set modulates visual areas: An event-related potential study of attentional capture. *Cognitive Brain Research*, 12, 383-395.

Bennett, P.J., and Pratt, J. (2001). The spatial distribution of inhibition of return. *Psychological Science, 12*, 76-80.

Berger, A., Henik, A., and Rafal, R. (2005). Competition between endogenous and exogenous orienting of visual attention. *Journal of Experimental Psychology: General, 134*, 207-221.

Boynton R.M., Kaiser P.K. (1968). Vision: the additivity law made to work for heterochromatic photometry with bipartite fields. *Science*, 161, 366–368.

Callaway, EM. (2005). Structure and function of parallel pathways in the primate early visual system. *Journal of Physiology, 566*, 13-19.

Carrasco, M., Ling, S., & Read, S. (2004). Attention alters appearance. *Nature Neuroscience, 7,* 308-313.

Cassagrande, V.A., and Xu, X. (2004). Parallel visual pathways: A comparative perspective In: *Visual Neurosciences,* (L. Chaupa and J. Werner Ed.), pp. 481-493, MIT.

Chambers, C. D., Payne, J. M., Stokes, M. G., & Mattingley, J. B. (2004). Fast and slow parietal pathways mediate spatial attention. *Nature Neuroscience, 7*, 217218.

Cole, G., Kentridge, R., & Heywood, C. (2005). Object onset and parvocellular guidance of attentional allocation. *Psychological Science, 16*, 270-274.

Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience, 3*, 201–215.

Desimone, R., & Duncan J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience, 18*, 193-222.

Di Russo, F., Martinez, A., & Hillyard, SA. (2003). Source analysis of event-related cortical activity during visuo-spatial attention. *Cerebral Cortex, 13*, 486-499.

Donchin, E. (1981). Surprise?…Surprise! *Psychophysiology, 18*, 493-513.

Eimer, M. (1993). Spatial cueing, sensory gating and selective response preparation: An ERP study of visuo-spatial orienting. *Electroencephalography and Clinical Neurophysiology, 88*, 408–420.

Ellemberg, D., Hammarrenger, B., Lepore, F., Roy, MS., & Guillemot, JP. (2001). contrast dependency of VEPs as a function of spatial frequency: the parvocellular and magnocellular contributions to human VEPs. *Spatial Vision, 15*, 9-111.

Folk, C. L., & Remington, R. [W.] (1999). Can new objects override attentional control settings? *Perception & Psychophysics*, 61, 727-739.

Folk, C., Remington, R. W., & Johnston, J. C. (1992). Involuntary covert orienting is contingent on attentional control settings. *Journal of Experimental Psychology: Human Perception and Performance, 18,* 1030-1044.

Folk, C. L., Remington, R. W., & Wright, J. H. (1994). The structure of attentional control: Contingent attentional capture by apparent motion, abrupt onset, and color. *Journal of Experimental Psychology: Human Perception & Performance*, 20, 317-329.

Fu, S., Fan, S., Chen, L., & Zhao, Y. (2001). The attentional effects of peripheral cueing as revealed by two event-related potential studies. *Clinical Neurophysiology, 112*, 172-185.

Gopfert, E., Muller, R., Breuer, D., and Greenlee, M.W. (1999). Similarities and dissimilarities between pattern VEPs and motion VEPs. *Documenta Ophthalmologica, 97*, 67-79.

Griffin, I.C., Miniussi, C., Nobre, A.C., 2002. Multiple mechanisms of selective attention: differential modulation of stimulus processing by attention to space or time *Neuropsychologia 40*, 2325–2340.

Hopfinger, J., and Mangun, G. R. (1998). Reflexive attention modulates processing of visual stimuli in human extrastriate cortex. *Psychological Science, 9,* 441-447.

Hopfinger, J. B., and Mangun, G. R. (2001). Tracking the influence of reflexive attention on sensory and cognitive processing. *Cognitive, Affective, & Behavioral Neuroscience, 1,* 56-65.

Hopfinger, J. B., and Ries, A. J. (2005). Automatic versus contingent mechanisms of sensory-driven neural biasing and reflexive attention. *Journal of Cognitive Neuroscience, 17,* 1341-1352.

Klistorner, A., Crewther, D.P., Crewther, S.G. (1998). Temporal analysis of the the chromatic flash VEP – separate colour and luminance contrast components. *Vision Research, 38*, 3979-4000.

Jasper, H. (1958). The ten twenty electrode system of the International Federation. *Electroencephalography and Clinical Neurophysiology, 10*, 371-375.

Jonides, J. and Yantis, S. (1988). Uniqueness of abrupt visual onset in capturing attention. *Perception and Psychophysics, 43*, 346-354.

Kaplan, E. (2004). The M, P, and K pathways of the primate visual system. In: *Visual Neurosciences,* (L. Chaupa and J. Werner Ed.), pp. 481-493, MIT.

Kaplan, E., and R.M. Shapley, 1986. The primate retina contains two types of ganglion cells, with high and low contrast sensitivity, *Proceedings of the National Academy of Science, USA,* 83, 2755-2757.

Kastner, S., & Ungerleider, L.G. (2000). Mechanisms of visual attention in the human cortex. *Annual Review of Neuroscience, 23*, 315-341.

Kenemans, JL., Kok, A. & Smulders, FL. (1993). Event-related potentials to conjunctions of spatial frequency and orientation as a function of stimulus parameters and response requirements. *Electroencepholography in Clinical Neurophysiollgy, 88*, 51-63.

Kulikowski, J.J., Robson, A.G., Murray, I.J. (2002). Scalp VEPs and intra-cortical responses to chromatic and achromatic stimuli in primates. *Documenta Ophthalmologica, 105*, 243-279.

Lamert, A., Wells, I., & Kean, M. (2003). Do isoluminant color changes capture attention. *Perception and Psychphysics, 65*, 495-507.

Lu, S. (2006). Cue duration and parvocellular guidance of visual attention. *Psychological Science, 17*, 101-102.

Luck, S.J., and Hillyard, S.A. (1994). Electrophysiological correlates of feature analysis during visual search. *Psychophysiology, 31*, 291-308.

Lupianez, J., et al., (Does IOR occur in discrimination tasks? Yes, but later. Perception And Psychophysics, 59, 1241-1254.

Mangun, G. R., & Hillyard, S. A. (1991). Modulation of sensory-evoked brain potentials provide evidence for changes in perceptual processing during visual–spatial priming.

Journal of Experimental Psychology: Human Perception and Performance, 17, 1057–1074.

Mangun, G. R., & Hillyard, S. A. (1995). Mechanisms and models of selective attention. in M. D. Rugg & M. G. H. Coles (Eds.), Electrophysiology of mind: Event-related brainpotentials and cognition (pp. 40–85). New York: Oxford.

Mangun, G.R., Hopfinger, J.B., Kussmaul, C.L., Fletcher, E., and Heinze, H.J. (1997). Covariations in ERP and PET measures of spatial selective attention in human extrastriate visual cortex. Human Brain Mapping, 5, 567-571.

Makeig, S., Westerfield, M., Townsend, J., Jung, TP., Courchesne, E., & Senjnowski, T.J. (1999). Functionally independent components of early event-related potentials in a visual spatial attention task. Philosophical Trans. Royal Society of London, 354, 1135-1144.

McDonald, J. J., Ward, L. M. & Kiehl, K. A. (1999). An event-related brain potential study of inhibition of return. *Perception & Psychophysics, 61*, 1411-1423.

Meredith, J.T. and Celesia, G.G. (1982). Pattern-reversal visual evoked potentials and Retinal eccentricity. *Electroencephalography Clinical Neurophysiology, 53*, 243-53.

Morrone, M.C., Denti, V., & Spinelli, D. (2002). Color and luminance contrasts attract independent attention. *Current Biology, 12(13),* 1134-1137.

Morrone, M.C., Denti, V., & Spinelli, D. (2004). Different attentional resources modulate the gain mechanisms for color and luminance contrast. *Vision Research, 44,* 1389-1401.

O'Donnell, BF., Swearer, JM., Smith, LT., Hokama, H., and McCarley, RW. (1997). A topographic study of ERPs elicited by visual feature discrimination. *Brain Topography, 10*, 133-143.

Posner, M.I. (1980). Orienting of attention. *Quarterly Journal of Experimental Psychology, 32*, 3-25.

Posner, M.I., and Cohen, Y. (1984). *Components of visual orienting*. In H. Bouma & D.G. Bouwhuis (Eds.), Attention and Performance X, (pp. 531-556). Hillsdale, NJ: Erlbaum.

Posner, M. I., Rafal, R. D., Choate, L. S., & Vaughan, J. (1985). Inhibition of return: Neural basis and function. *Cognitive Neuropsychology, 2*, 211–228.

Potts, Geoffery. (2004). An ERP index of task relevance evaluation of visual stimuli. *Brain and Cognition, 56*, 5-13.

Pratt, J., Hillis, J., Gold, J.M. (2001). The effect of the physical characteristics of cues And targets on facilitation and inhibition. *Psychonomic Bulletin & Review, 8*, 489-495.

Prime, D. J., & Ward, L. M. (2004). Inhibition of return from stimulus to response. *Psychological Science, 15*, 272–276.

Prime, D. J., & Ward, L. M. (2006). Cortical expressions of inhibition of return. *Brain Research, 1072*, 161–174.

Proverbio, A.M., Zani, A., and Mangun, G.R. (1993). Electrophysiological substrates of selective attention to spatial frequency. *Bull. Psychonom. Soc,* 31, 368.

Rafal, R.D. et al., (1989). Saccade preparation inhibits reorienting to recently attended locations. *Journal of Experimental Psychology: Human Perception and Performance, 15*, 673-685.

Reed, J.L., Marx, M.S. and May, J.G. (1984). Spatial frequency tuning in the visual evoked Potential elicited by sine-wave gratings. *Vision Research, 24,* 1057-1062.

Ruchkin, D., Johnson, R., Canoune, H., Ritter, W., & Hammer, M. (1990). Multiple sources of P3b associated with different types of information. *Psychophysiology, 27,* 157- 176.

Skandies, W. (1984). Scalp potential fields evoked by grating stimuli: effects of spatial frequency and orientation. *Electroenceph. Clin. Neurophysiology, 58*, 325-332.

Smith, V.C., Pororny, J. (1975). Spectral sensitivity of the foveal cone photopigments between 400 and 500 nm. *Vision Research, 15*, 161-172.

Snowden, R.J. (2002). Visual attention to color: Parvocellular guidance of attentional resources? *Psychological Science, 13*, 180–184.

Song, Wei-qun, Li, Xinying, Luo, Yue-Jia, Du, Bo-qi, & Ji, Xun-ming. (2006).Brain dynamic mechanisms of scale effect in visual spatial attention. *Neuroreport*, 17, 1643-1647.

Sumner, P., Adamjee, T., & Mollon, J.D. (2002). Signals invisible to the collicular and magnocellular pathways can capture visual attention. *Current Biology, 12*, 1312–1316.

Steinman, B., Steinman, S., Lehmkuhle, S. (1997). Transient visual attention is dominated by the magnocellular stream. *Vision Research, 37*, 17-23.

Taylor, T. L., & Klein, R. M. (1998). On the causes and effects of inhibition of return. *Psychonomic Bulletin & Review, 5*, 625–643.

Taylor, T. L., & Klein, R. M. (2000). Visual and motor effects in inhibition of return. *Journal of Experimental Psychology: Human Perception and Performance, 26*, 1639–1656.

Theeuwes, J. (1995). Abrupt luminance change pops out; abrupt color change does not. *Perception & Psychophysics, 57*, 637–644.

Tipper, S. (2004). Ch. 45 Action and Attention. In: *Cognitive Neurosciences III.* (M. Gazzaniga Ed.), pp. 619-629, MIT.

Tsalma, D., Slagter, HA., Nieuwenhuis, JH., and Kok, A. (2005). The orienting of visuospatial attention: An event-related brain potential study. *Cognitive Brain Research, 25*, 117-129.

Van Voorhis, S. T., & Hillyard, S. A. (1977). Visual evoked potentials and selective attention to points in space. *Perception & Psychophysics, 22*, 54–62.

Wicken&, Kramer, A., Vanesse, L., & Donchin, E. (1983). The performance of concurrent tasks: a psychophysiological analysis of the reciprocity of information processing resources. *Science, 221,* 1080-1082**.**

Woldorff, M. G. (1993). Distortion of ERP averages due to overlap from temporally adjacent ERPs: Analysis and correction. *Psychophysiology, 30*, 98–119.

Yantis, S. and Jonides, J. (1984). Abrupt visual onsets and selective attention: Evidence from visual search. *Journal of Experimental Psychology: Human Perception and Performance, 5*, 625-638.

Yeshurun, Y. (2004). Isoluminant stimuli and re background attenuate the effects of Transient spatial attention on temporal resolution. *Vision Research, 44*, 1375-1387.